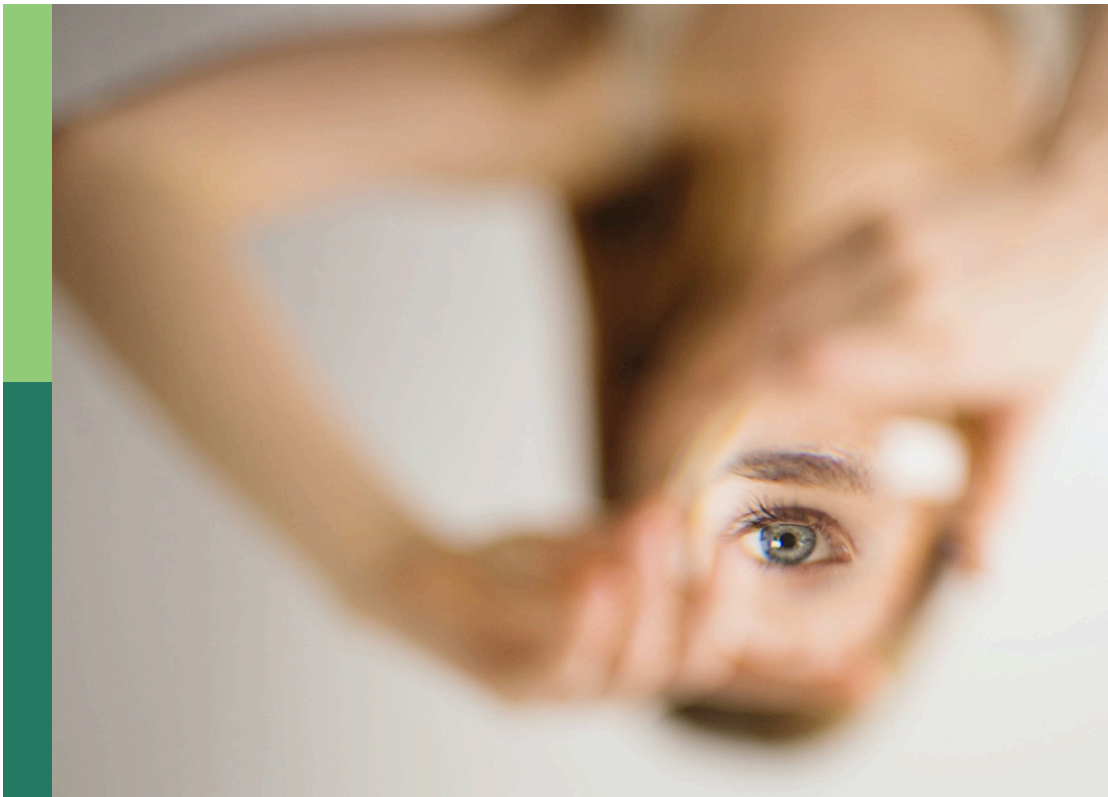
frontiers | Research Topics

Insights in emotion science

Edited by
Florin Dolcos, Andrew Kemp and Alfons O. Hamm

Published in
Frontiers in Psychology



ISSN 1664-8714
ISBN 978-2-8325-6445-5
DOI 10.3389/978-2-8325-6445-5

About Frontiers

Frontiers is more than just an open access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers journal series

The Frontiers journal series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the *Frontiers journal series* operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews. Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view. By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the *Frontiers journals series*: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area.

Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers editorial office: frontiersin.org/about/contact

Insights in emotion science

Topic editors
Florin Dolcos — University of Illinois at Urbana-Champaign, United States
Andrew Kemp — Swansea University, United Kingdom
Alfons O. Hamm — University of Greifswald, Germany

Citation
Dolcos, F., Kemp, A., Hamm, A. O., eds. (2025). *Insights in emotion science*.
Lausanne: Frontiers Media SA. doi: 10.3389/978-2-8325-6445-5

Table of contents

frontiers | Frontiers in Psychology

TYPE Perspective
PUBLISHED 16 November 2023
DOI 10.3389/fpsyg.2023.1254179

OPEN ACCESS

EDITED BY
Andrew Kemp,
Swansea University, United Kingdom

REVIEWED BY
Eldad Yechiam,
Technion Israel Institute of Technology, Israel

*CORRESPONDENCE
Melissa T. Buelow
✉ buelow.11@osu.edu

RECEIVED 06 July 2023
ACCEPTED 31 October 2023
PUBLISHED 16 November 2023

CITATION
Buelow MT, Moore S, Kowalsky JM and Okdie BM (2023) Cognitive chicken or the emotional egg? How reconceptualizing decision-making by integrating cognition and emotion can improve task psychometrics and clinical utility.
Front. Psychol. 14:1254179.
doi: 10.3389/fpsyg.2023.1254179

Cognitive chicken or the emotional egg? How reconceptualizing decision-making by integrating cognition and emotion can improve task psychometrics and clinical utility

Melissa T. Buelow[1]*, Sammy Moore[2], Jennifer M. Kowalsky[1] and Bradley M. Okdie[1]

[1]Department of Psychology, The Ohio State University, Newark, OH, United States, [2]School of Psychological Sciences, The University of Western Australia, Perth, WA, Australia

Decision-making is an executive function, tapping into cognitive, emotional, and personality-based components. This complexity, and the varying operational definitions of the construct, is reflected in the rich array of behavioral decision-making tasks available for use in research and clinical settings. In many cases, these tasks are "subfield-specific," with tasks developed by cognitive psychologists focusing on cognitive aspects of decision-making and tasks developed by clinical psychologists focusing on interactions between emotional and cognitive aspects. Critically, performance across different tasks does not consistently correlate, obfuscating the ability to compare scores between measures and detect changes over time. Differing theories as to what cognitive and/or emotional aspects affect decision-making likely contribute to this lack of consistency across measures. The low criterion-related validity among decision-making tasks and lack of consistent measurement of the construct presents challenges for emotion and decision-making scholars. In this perspective, we provide several recommendations for the field: (a) assess decision-making as a specific cognitive ability versus a taxonomy of cognitive abilities; (b) a renewed focus on convergent validity across tasks; (c) further assessment of test–retest reliability versus practice effects on tasks; and (d) reimagine future decision-making research to consider the research versus clinical implications. We discuss one example of decision-making research applied to clinical settings, acquired brain injury recovery, to demonstrate how some of these concerns and recommendations can affect the ability to track changes in decision-making across time.

KEYWORDS

decision-making, emotion, cognition, executive function, validity

1. Introduction

Decision-making belongs to a group of higher-order, complex cognitive abilities linked to the prefrontal cortex (PFC) (Lezak et al., 2004) known as executive functions (EF). Decisions that are more emotion-based often activate ventromedial prefrontal cortex (VMPFC) (Ernst et al., 2002; Cho et al., 2012; Paulsen et al., 2012), whereas decisions that are more cognition-based activate dorsolateral prefrontal cortex (DLPFC) (Krain et al., 2006; Rolls and Grabenhorst, 2008). Yet both VMPFC and DLPFC can contribute to either type of decision-making. The brain's reward pathway links the PFC with the limbic system and midbrain (Glimcher et al., 2009; Galvan, 2012), and decision-making activates this pathway (Jessor, 1991; Elliott et al., 2008; Curtis and Lee, 2010; Reyna, 2012). But aspects of the limbic system (Dalgleish, 2004; Fossati, 2012) and PFC (Baker et al., 1997) are linked to the processing of emotions, demonstrating that cognition and emotion utilize similar circuitry. Should we disentangle cognition and emotion in decision-making, or do we need to consider these two components together when defining the construct? It is possible that keeping emotion out of cognition (and vice versa) when defining decision-making has led to some of the current issues affecting the field. In the following sections, we provide a review of the current status of several important issues for decision-making as an individual differences variable and provide recommendations for the field moving forward. As applicable, we discuss where there may be different needs for those in the research versus clinical realms.

2. Specificity versus taxonomy of decision-making

Although a full review of the history of decision-making, and all the relevant theories of it, is outside the scope of this perspective, several reviews and key pieces are available regarding signal detection theory (Stanislaw and Todorov, 1999), expected value- and utility-based theories (Von Neumann and Morgenstern, 1944; Machina, 1987), prospect theory (Kahneman and Tversky, 1979), and dual (Tversky and Kahneman, 1983; Metcalfe and Mischel, 1999; Reyna, 2004; Evans, 2008) and triple (Wood and Bechara, 2014) process system theories of decision-making. A key component of several of these theories is the extent to which utilizing cognitive factors (e.g., working memory, knowledge of probabilities, abstract reasoning; Reyna et al., 2009; Weber and Johnson, 2009; Curtis and Lee, 2010; Reyna and Brainerd, 2011; Brand et al., 2014) and emotional factors (Suhr and Tsanadis, 2007; Roiser et al., 2009; Buelow et al., 2013) can affect decisions. A differing emphasis on emotion versus cognition can lead to differences in the overall conceptualization of decision-making and, subsequently, in how it is assessed.

Is decision-making a specific cognitive ability, or does it instead represent a taxonomy of related cognitive abilities that are tied to the PFC, limbic system, and their subcortical connections? Is decision-making similar to the other executive functions, in that it is made up of different aspects of the construct rather than one overarching ability that is applied in every situation? To the extent that a decision is made in a consistent manner, across situations and across time, then decision-making may be more of a specific cognitive ability. Yet as many show (e.g., Schoemaker, 1993; Ert and Yechiam, 2010; Figner and Weber, 2011; Yechiam and Ert, 2011), individuals do not consistently weigh gains and losses (or risks and benefits) across situations. How questions are worded/framed (e.g., gain-framing versus loss-framing; Tversky and Kahneman, 1981; Yechiam and Ert, 2011) can lead to different decisions. These inconsistencies may also occur based on the specific type of risk, the extent to which cognitive and emotional factors come into play, and one's own risk-taking propensity (e.g., Figner and Weber, 2011). These inconsistencies lead us to wonder if decision-making mimics executive functions, in that it serves as a taxonomy for a series of 'subcomponents' that make up the overarching construct. Several of these subcomponents may be activated in one situation but not in another, which could account for the inconsistencies when performance is assessed across tasks. Moving forward, the field should consider the overarching construct of decision making and whether it is a specific ability or a higher-order classification for a set of cognitive abilities.

3. Convergent validity across tasks

If decision-making is a specific cognitive ability, and did not represent a taxonomy like the executive functions, then tasks assessing decision-making should show strong convergent validity. A task such as the Iowa Gambling Task (IGT; Bechara et al., 1994) should show strong correlations with the Balloon Analog Risk Task (BART; Lejuez et al., 2002), Game of Dice Task (GDT; Brand et al., 2007), and others. Some previous research finds such correlations (Brand et al., 2007; Henninger et al., 2010; Koritzky and Yechiam, 2010; Upton et al., 2011; MacKillop et al., 2014; Brown et al., 2015), but most instead show weak/small (Skeel et al., 2007; Mäntylä et al., 2012; Brunell and Buelow, 2017) or no (Mäntylä et al., 2012; Pletzer and Ortner, 2016) correlations between decision-making tasks designed to assess individual differences in the construct. If decision-making instead represents a taxonomy of cognitive abilities, then these inconsistencies make sense. Tasks that pull for more "cold" executive functions may correlate more with each other than with tasks that pull more for "hot" executive functions. We see this relationship when assessing correlations between the Wisconsin Card Sort Task, a measure of cold EF linked to the DLPFC (Lezak et al., 2004), as it correlates with decision-making tasks assessing more cold cognitions (e.g., Columbia Card Task, GDT; Brand et al., 2007, 2014; Buelow, 2015) but not with more hot/emotion-based tasks (e.g., IGT; Bechara et al., 2001; Reynolds et al., 2019). Factor analyses also demonstrate this lack of convergent validity (Buelow and Blaine, 2015).

Research investigating cognitive models of decisions on behavioral tasks point toward a better understanding of decision-making and convergent validity across tasks. Previous research points to factors such as sensitivity to gains/rewards (Yechiam and Busemeyer, 2008; Ert and Yechiam, 2010; Brevers et al., 2014), sensitivity to losses/risks (Bishara et al., 2009; Ert and Yechiam, 2010), frequency of gains and losses (Lin et al., 2009), choice consistency (Stout et al., 2004; Yechiam et al., 2005; Lin et al., 2016), discounting of versus learning from feedback (Yechiam et al., 2005; Prause and Lawyer, 2014; Byrne and Worthy, 2016), and individual differences in risk perception and acceptance (Wallsten et al., 2005; Ert and Yechiam, 2010; Figner and Weber, 2011; Yechiam and Ert, 2011) can affect decision-making across multiple tasks. It is possible that the relative lack of convergent validity across tasks to date is partly due to the nature of decision-making itself (e.g., specificity versus taxonomy) and partly due to the use of total/net scores to assess decision-making. Future research should continue to investigate these cognitive modeling-based commonalities across tasks, as there may be more convergence than it appears.

4. Test–retest reliability

How does performance on decision-making tasks change across time? Is decision-making a relatively stable construct, or does it change across time or based on other factors? To assess the stability of decision-making, we can assess the test–retest reliability of various behavioral tasks. Estimates of test–retest reliability vary across specific tasks, samples, and time periods, but overall there are often moderate to strong correlations between tasks administered days (Johnson and Bruner, 2013; Weafer et al., 2013), weeks (Buelow and Barnhart, 2018), months (Forster et al., 2016; Peng et al., 2018), and years (Kirby, 2009; Yechiam and Ert, 2011) apart. Although these correlations are relatively high, interpretation of them as evidence in favor of strong test–retest reliability depends on the context. Portney and Watkins (2015)'s guidelines for clinical measures are that correlations across time of 0.50–0.75 are poor/moderate while those over 0.75 are acceptable. Few—if any—of these correlations meet that criterion. In addition, there are some tasks that are single-use, as there is some element (e.g., learning the risks/benefits of the decks on the IGT) that cannot be 'unlearned' to allow for a second, future administration. On the IGT in particular, evidence of these learned practice effects is evident even years after the initial administration (e.g., Waters-Wood et al., 2012; see Buelow, 2020, for review). Although lab-based studies of healthy control or clinical participants may require a one-time assessment of current decision-making skills, real-world clinical evaluations can require multiple assessments over time. Tracking decision-making over time is difficult when (a) tasks lack test–retest reliability and convergent validity and (b) there are no clinically-available tasks (i.e., those that have been validated in clinical samples and for which normative data is available) that can be used in a longitudinal assessment. As we will discuss in the next section, concerns about reliability and validity may differ based on the implications of a research study.

5. Reliability, validity, and experimental designs

As the field of decision science moves forward, the noted concerns about reliability and validity can point in different directions for new experimental designs, in part due to the basis for or reasoning behind a new research study. Is the intent to predict behavior? Document impaired decision-making based on a situational factor, individual differences factor, or psychological or medical/neurological diagnosis? Assess potential for change in the future? Understand decision-making or other cognitive/emotional process? Although in some cases it may be sufficient to document a one-time only assessment of decision-making impairment due to a diagnosis or other factor, in other cases the findings may have implications for treatments to improve decision-making skills among, for example, those with an acquired brain injury.

Acquired brain injury (ABI) is one example where more research is needed into both test–retest reliability and convergent validity, as tracking changes in cognitive difficulties across time is important for the patient with an ABI. ABI refers to any injury to the brain, such as what occurs in the course of traumatic (TBI; e.g., from accidents or falls) or nontraumatic (e.g., stroke) injury (Cullen et al., 2008). Although cognitive and emotional consequences of ABI vary due to the specific regions affected, the PFC is often negatively impacted (McAllister, 2011). Following ABI, patients may experience difficulties with attention, memory encoding and retrieval, processing speed, and EF (Allanson et al., 2017; Watson et al., 2020); however, these cited meta-analyses do not assess how hot EFs, such as decision-making, change post-ABI. Many clinically-available EF tasks focus on cold cognitive processes, even though OFC, VMPFC, and medial PFC may also be affected. Results of EF assessments predict long-term outcome for patients post-ABI (Allanson et al., 2017), yet this is often predicated on results of cold (non-emotion based) EF assessment. Individuals with ABI can also experience changes in emotional experience and expression (Gouick and Gentleman, 2004; de Sousa et al., 2012; with Phineas Gage as an early example).

In their Jose et al. (2020) review, Jose and colleagues examined the current understanding of EF in ABI. They divided decision-making into a set of skills that include value coding, social context, and emotional dysregulation, with moral reasoning and working memory as related cognitive functions. Research suggests that VMPFC, DLPFC, and OFC are involved in each of these decision-making components, despite the belief that each structure is specific to one cognitive (or emotional) function. They point out that focusing on a specific/small area of cognition can result in a loss of the bigger picture in ABI, such as by focusing on value coding one loses sight of the working memory and emotion regulation difficulties that could also affect decision-making.

Following ABI, individuals are typically assessed in the acute recovery phase to (a) predict pre-morbid functioning; (b) determine their strengths and weaknesses post-injury; and (c) develop a treatment plan. This gives a single snapshot of that individual's cognitive history, yet it is often used for future comparison. Although important to identify cognitive deficits, it is also important to document if those deficits resolve. The IGT is currently the only behavioral task with available normative data to guide interpretation of task performance in clinical populations (Bechara, 2007), with a recent meta-analysis supporting its utility to assess decision-making impairments post-ABI (regardless of lesion location; Moore et al., 2023, under review)[1]. However, even 1+ years after initial assessment, practice effects remain (not specific to ABI samples; Tuvblad et al., 2013; Xiao et al., 2013). If there were additional tasks that demonstrated strong convergent validity with the IGT, they could instead be used to assess decision-making change over time. But there is a lack of convergent validity across decision-making tasks, creating difficulty showing improved decision-making as individuals recover from ABI. And while there is a typical recovery period post-ABI, especially from traumatic etiologies (Cullen et al., 2008), our inability to track decision-making changes

---

[1] Moore, S., Naragon-Gainey, K., Pestell, C.F., Becerra, R., Buelow, M.T., and Fynn, D.M. (2023). The level and nature of impairment on the Iowa gambling task following acquired brain injury: a meta-analysis. (under review).

across time limits what we can learn about EF recovery and how decision-making strategies may change post-ABI.

Outside of ABI and other clinical diagnoses where repeatable decision-making tasks can be of benefit, within-subjects study designs can also benefit from repeatable tasks. As just one example, multiple studies have shown that participants' current mood or emotional state can affect decision-making (e.g., Mitchell and Phillips, 2007; Tamir and Robinson, 2007; Buelow et al., 2013; Forgas, 2013). In most of the lab-based manipulations of mood, decision-making was assessed post-manipulation only. If there was a repeatable decision-making task, it could be utilized in a pre-post manipulation, within-participant study design. This would additionally allow researchers to assess the extent to which the mood manipulation interacted with prior characteristics of the individual and their decision-making ability to affect subsequent performance.

6. Conclusion

The cognitive and emotional conceptualizations of decision-making need to be more precise: when should cognition and emotion be integrated, and when should they be assessed separately? Applications of dual process theory suggest cognition and emotion inform each other, but many current tasks rely on operational definitions of decision-making focused on only cognition or only emotion. Emotion can inform our understanding of cognition, and cognition can inform our understanding of emotion. VMPFC and DLPFC pathways are functionally connected, forming a prefrontal-cingulate cortex network that combines elements of hot and cold ("hot-cold") decision-making (Jose et al., 2020; Salehinejad et al., 2021). Even tasks designed to examine emotion-based decision-making are correlated with measures of EFs and other cognitive abilities, indicating you cannot take cognition out of emotion either. Continuing to 'silo' cognitive and emotional theories of decision-making limits our ability to understand why individuals take risks and make suboptimal decisions. Utilizing an integrated conceptualization of decision-making and better centering it within other EFs may help researchers develop new tasks with adequate psychometrics that can be used to track recovery from an acute TBI, for example.

We believe the field of decision science still has much to offer our understanding of decision-making processes. However, the field's impact is constrained by the lack of good psychometrics for many tasks and inconsistencies in conceptualizations of decision-making leading to differences in explaining task performance. The incorporation of cognitive and affective components of decision-making into a single taxonomy will methodologically increase reliability and validity of decision-making measures, as tasks born out of this conceptualization should, at their core, be assessing an overarching conceptualization that includes the assessment of both cognitive and affective components of decision-making.

Author contributions

MB: Conceptualization, Writing – original draft, Writing – review & editing. SM: Conceptualization, Writing – review & editing. JK: Conceptualization, Writing – review & editing. BO: Conceptualization, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Allanson, F., Pestell, C., Gignac, G. E., Yeo, Y. X., and Weinborn, M. (2017). Neuropsychological predictors of outcome following traumatic brain injury in adults: a meta-analysis. *Neuropsyhol. Rev.* 27, 187–201. doi: 10.1007/s11065-017-9353-5

Baker, S. C., Frith, C. D., and Dolan, R. J. (1997). The interaction between mood and cognitive function studied with PET. *Psychol. Med.* 27, 565–578. doi: 10.1017/S0033291797004856

Bechara, A. (2007). *Iowa gambling task professional manual.* Lutz, FL: Psychological Assessment Resources.

Bechara, A., Damasio, A. R., Damasio, H., and Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition* 50, 7–15. doi: 10.1016/0010-0277(94)90018-3

Bechara, A., Dolan, S., Denburg, N., Hindes, A., Anderson, S. W., and Nathan, P. E. (2001). Decision-making deficits, linked to a dysfunctional ventromedial prefrontal cortex, revealed in alcohol and stimulant abusers. *Neuropsycholgia* 39, 376–389. doi: 10.1016/S0028-3932(00)00136-6

Bishara, A. J., Pleskac, T. J., Fridberg, D. J., Yechiam, E., Lucas, J., Busemeyer, J. R., et al. (2009). Similar processes despite divergent behavior in two commonly used measures of risky decision making. *J. Behav. Decis. Mak.* 22, 435–454. doi: 10.1002/bdm.641

Brand, M., Recknor, E. C., Grabenhorst, F., and Bechara, A. (2007). Decisions under ambiguity and decisions under risk: correlations with executive functions and comparisons of two different gambling tasks with implicit and explicit rules. *J. Clin. Exp. Neuropsychol.* 29, 86–99. doi: 10.1080/13803390500507196

Brand, M., Schiebener, J., Pertl, M.-T., and Delazer, M. (2014). Know the risk, take the win: how executive functions and probability processing influence advantageous decision making under risk conditions. *J. Clin. Exp. Neuropsychol.* 36, 914–929. doi: 10.1080/13803395.2014.955783

Brevers, D., Koritzky, G., Bechara, A., and Noël, X. (2014). Cognitive processes underlying impaired decision-making under uncertainty in gambling disorder. *Addict. Behav.* 39, 1533–1536. doi: 10.1016/j.addbeh.2014.06.004

Brown, E. C., Hack, S. M., Gold, J. M., Carpenter, W. T., Fischer, B. A., Prentice, K. P., et al. (2015). Integrating frequency and magnitude information in decision-making in schizophrenia: an account of patient performance on the Iowa gambling task. *J. Psychiatr. Res.* 66-67, 16–23. doi: 10.1016/j.jpsychires.2015.04.007

Brunell, A. B., and Buelow, M. T. (2017). Narcissism and performance on behavioral decision-making tasks. *J. Behav. Decis. Mak.* 30, 3–14. doi: 10.1002/bdm.1900

Buelow, M. T. (2015). Predicting performance on the Columbia card task: effects of personality characteristics, mood, and executive functions. *Assessment* 22, 178–187. doi: 10.1177/1073191114539383

Buelow, M.T. (2020). *Risky decision making in psychological disorders*. London: Elsevier

Buelow, M. T., and Barnhart, W. R. (2018). Test-retest reliability of common behavioral decision making tasks. *Arch. Clin. Neuropsychol.* 33, 125–129. doi: 10.1093/arclin/acx038

Buelow, M. T., and Blaine, A. L. (2015). The assessment of risky decision making: a factor analysis of performance on the Iowa gambling task, balloon analogue risk task, and Columbia card task. *Psychol. Assess.* 27, 777–785. doi: 10.1037/a0038622

Buelow, M. T., Okdie, B. M., and Blaine, A. L. (2013). Seeing the forest through the trees: improving decision making on the Iowa gambling task by shifting focus from short- to long-term outcomes. *Front. Psychol.* 4:773. doi: 10.3389/fpsyg.2013.00773

Byrne, K. A., and Worthy, D. A. (2016). Toward a mechanistic account of gender differences in reward-based decision-making. *J. Neurosci. Psychol. Econ.* 9, 157–168. doi: 10.1037/npe0000059

Cho, S. S., Pellecchia, G., Aminian, K., Ray, N., Segura, B., Obeso, I., et al. (2012). Morphometric correlation of impulsivity in medial prefrontal cortex. *Brain Topogr.* 26, 479–487. doi: 10.1007/s10548-012-0270-x

Cullen, N. K., Park, Y., and Bayley, M. T. (2008). Functional recovery following traumatic vs non-traumatic brain injury: a case-controlled study. *Brain Inj.* 22, 1013–1020. doi: 10.1080/02699050802530581

Curtis, C. E., and Lee, D. (2010). Beyond working memory: the role of persistent activity in decision making. *Trends Cogn. Sci.* 14, 216–222. doi: 10.1016/j.tics.2010.03.006

Dalgleish, T. (2004). The emotional brain. *Nat. Rev. Neurosci.* 5, 583–589. doi: 10.1038/nrn1432

de Sousa, A., McDonald, S., and Rushby, J. (2012). Changes in emotional empathy, affective responsivity, and behavior following severe traumatic brain injury. *J. Clin. Exp. Neuropsychol.* 34, 606–623. doi: 10.1080/13803395.2012.667067

Elliott, R., Agnew, Z., and Deakin, F. W. (2008). Medial orbitofrontal cortex codes relative rather than absolute value of financial rewards in humans. *Eur. J. Neurosci.* 27, 2213–2218. doi: 10.1111/j.1460-9568.2008.06202.x

Ernst, M., Bolla, K., Mouratidis, M., Contoreggi, C., Matochik, J. A., Kurian, V., et al. (2002). Decision-making in a risk-taking task: A PET study. *Neuropsychopharmacology* 26, 682–691. doi: 10.1016/S0893-133X(01)00414-6

Ert, E., and Yechiam, E. (2010). Consistent constructs in individuals' risk taking in decisions from experience. *Acta Psychol.* 134, 225–232. doi: 10.1016/j.actpsy.2010.02.003

Evans, J. S. B. T. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annu. Rev. Psychol.* 59, 255–278. doi: 10.1146/annurev.psych.59.103006.093629

Figner, B., and Weber, E. U. (2011). Who takes risks when and why?: determinants of risk taking. *Curr. Dir. Psychol. Sci.* 20, 211–216. doi: 10.1177/0963721411415790

Forgas, J. P. (2013). Don't worry, be sad! On the cognitive, motivational, and interpersonal benefits of negative mood. *Curr. Dir. Psychol. Sci.* 22, 225–232. doi: 10.1177/0963721412474458

Forster, S. E., Finn, P. R., and Brown, J. W. (2016). A preliminary study of longitudinal neuroadaptation associated with recovery from addiction. *Drug Alcohol Depend.* 168, 52–60. doi: 10.1016/j.drugalcdep.2016.08.626

Fossati, P. (2012). Neural correlates of emotion processing: from emotional to social brain. *Eur. Neuropsychopharmacol.* 22, S487–S491. doi: 10.1016/j.euroneuro.2012.07.008

Galvan, A. (2012). "Risky behavior in adolescents: the role of the developing brain" in *The adolescent brain: Learning, reasoning, and decision making*. eds. V. F. Reyna, S. B. Chapman, M. R. Dougherty and J. Confrey (Washington, DC: American Psychological Association), 267–289.

Glimcher, P.W., Camerer, C.F., Fehr, E., and Poldrack, R.A.. (2009). *Neuroeconomics: Decision making and the brain*. New York: Academic Press.

Gouick, J., and Gentleman, D. (2004). The emotional and behavioural consequences of traumatic brain injury. *Trauma* 6, 285–292. doi: 10.1191/1460408604ta323oa

Henninger, D. E., Madden, D. J., and Huettel, S. A. (2010). Processing speed and memory mediate age-related differences in decision making. *Psychol. Aging* 25, 262–270. doi: 10.1037/a0019096

Jessor, R. (1991). Risk behavior in adolescence: a psychosocial framework for understanding and action. *J. Adolesc. Health* 12, 597–605. doi: 10.1016/1054-139X(91)90007-K

Johnson, M. W., and Bruner, N. R. (2013). Test-retest reliability and gender differnces in the sexual discounting task among cocaine-dependent individuals. *Exp. Clin. Psychopharmacol.* 21, 277–286. doi: 10.1037/a0033071

Jose, R. G., Samuel, A. S., and Isabel, M. M. (2020). Neuropsychology of executive functions in patients with focal lesion in the prefrontal cortex: a systematic review. *Brain Cogn.* 146:105633. doi: 10.1016/j.bandc.2020.105633

Kahneman, D., and Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–292. doi: 10.2307/1914185

Kirby, K. N. (2009). One-year temporal stability of delay-discount rates. *Psychon. Bull. Rev.* 16, 457–462. doi: 10.3758/PBR.16.3.457

Koritzky, G., and Yechiam, E. (2010). On the robustness of description and experience based decision tasks to social desirability. *J. Behav. Decis. Mak.* 23, 83–99. doi: 10.1002/bdm.660

Krain, A. L., Wilson, A. M., Arbuckle, R., Castellanos, F. X., and Milham, M. P. (2006). Distinct neural mechanisms of risk and ambiguity: a meta-analysis of decision-making. *NeuroImage* 32, 477–484. doi: 10.1016/j.neuroimage.2006.02.047

Lejuez, C. W., Richards, J. B., Read, J. P., Kahler, C. W., Ramsey, S. E., Stuart, G. L., et al. (2002). Evaluation of a behavioral measure of risk taking: the balloon analogue risk task (BART). *J. Exp. Psychol. Appl.* 8, 75–84. doi: 10.1037//1076-898x.8.2.75

Lezak, M.D., Howieson, D.B., and Loring, D.W. (2004). *Neuropsychological Assessment*. Oxford: Oxford University Press

Lin, C. H., Chiu, Y. C., and Huang, J. T. (2009). Gain-loss frequency and final outcome in the Soochow gambling task: a reassessment. *Behav. Brain Funct.* 5:45. doi: 10.1186/1744-9081-5-45

Lin, C. H., Lin, Y. K., Song, T. J., Huang, J. T., and Chiu, Y. C. (2016). A simplified model of choice behavior under uncertainty. *Front. Psychol.* 7:1201. doi: 10.3389/fpsyg.2016.01201

Machina, M. (1987). Choice under uncertainty: problems solved and unsolved. *J. Econ. Perspect.* 1, 121–154. doi: 10.1257/jep.1.1.121

MacKillop, J., Miller, J. D., Fortune, E., Maples, J., Lance, C. E., Campbell, W. K., et al. (2014). Multidimensional examination of impulsivity in relation to disordered gambling. *Exp. Clin. Psychopharmacol.* 22, 176–185. doi: 10.1037/a0035874

Mäntylä, T., Still, J., Gullberg, S., and Del Missier, F. (2012). Decision making in adults with ADHD. *J. Atten. Disord.* 16, 164–173. doi: 10.1177/1087054709360494

McAllister, T. W. (2011). Neurobiological consequences of traumatic brain injury. *Dialogues Clin. Neurosci.* 13, 287–300. doi: 10.31887/DCNS.2011.13.2/tmcallister

Metcalfe, J., and Mischel, W. (1999). A hot/cool-system analysis of delay of gratification: dynamics of willpower. *Psychol. Rev.* 106, 3–19. doi: 10.1037/0033-295X.106.1.3

Mitchell, R. L. C., and Phillips, L. H. (2007). The psychological, neurochemical and functional neuroanatomical mediators of the effects of positive and negative mood on executive functions. *Neuropsychologia* 45, 617–629. doi: 10.1016/j.neuropsychologia.2006.06.030

Paulsen, D. J., Carter, R. M., Platt, M. L., Huettel, S. A., and Brannon, E. M. (2012). Neurocognitive development of risk aversion from early childhood to adulthood. *Front. Hum. Neurosci.* 5:178. doi: 10.3389/fnhum.2011.00178

Peng, J., Feng, T., Zhang, J., Zhao, L., Zhang, Y., Chang, Y., et al. (2018). Measuring decision-making competence in Chinese adults. *J. Behav. Decis. Mak.* 32, 266–279. doi: 10.1002/bdm.2114

Pletzer, B., and Ortner, T. M. (2016). Neuroimaging supports behavioral personality assessment: overlapping activations during reflective and impulsive risk taking. *Biol. Psychol.* 119, 46–53. doi: 10.1016/j.biopsycho.2016.06.012

Portney, L.G., and Watkins, M.P. (2015). *Foundations of clinical research: applications to practice*. Pearson/Prentice Hall. Upper Saddle River.

Prause, N., and Lawyer, S. (2014). Specificity of reinforcement for risk behaviors of the balloon analogue risk task using math models of performance. *J. Risk Res.* 17, 317–335. doi: 10.1080/13669877.2013.808688

Reyna, V. F. (2004). How people make decisions that involve risk: a dual-processes approach. *Curr. Dir. Psychol. Sci.* 13, 60–66. doi: 10.1111/j.0963-7214.2004.00275.x

Reyna, V. F. (2012). A new intuitionism: meaning, memory, and development in fuzzy-trace theory. *Judgm. Decis. Mak.* 7, 332–359. doi: 10.1017/S1930297500002291

Reyna, V. F., and Brainerd, C. J. (2011). Dual processes in decision making and developmental neuroscience: A fuzzy-trace model. *Dev. Rev.* 31, 180–206. doi: 10.1016/j.dr.2011.07.004

Reyna, V. F., Nelson, W. L., Han, P. K., and Dieckmann, N. F. (2009). How numeracy influences risk comprehension and medical decision making. *Psychol. Bull.* 135, 943–973. doi: 10.1037/a0017327

Reynolds, B. W., Basso, M. R., Miller, A. K., Whiteside, D. M., and Combs, D. (2019). Executive function, impulsivity, and risky behaviors in young adults. *Neuropsychology* 33, 212–221. doi: 10.1037/neu0000510

Roiser, J., Farmer, A., Lam, D., Burke, A., O'Neill, N., Keating, S., et al. (2009). The effect of positive mood induction on emotional processing in euthymic individuals with bipolar disorder and controls. *Psychol. Med.* 39, 785–791. doi: 10.1017/S0033291708004200

Rolls, E. T., and Grabenhorst, F. (2008). The orbitofrontal cortex and beyond: from affect to decision-making. *Prog. Neurobiol.* 86, 216–244. doi: 10.1016/j.pneurobio.2008.09.001

Salehinejad, M. A., Ghanavati, E., Rashid, M. H. A., and Nitsche, M. A. (2021). Hot and cold executive functions in the brain: a prefrontal-cingular network. *Brain Neurosci. Adv.* 5, 239821282110077–239821282110019. doi: 10.1177/23982128211007769

Schoemaker, P. J. H. (1993). Determinants of risk-taking: behavioral and economic views. *J. Risk Uncert.* 6, 49–73. doi: 10.1007/BF01065350

Skeel, R. L., Neudecker, J., Pilarski, C., and Pytlak, K. (2007). The utility of personality variables and behaviorally-based measures in the prediction of risk-taking behavior. *Personal. Individ. Differ.* 43, 203–214. doi: 10.1016/j.paid.2006.11.025

Stanislaw, H., and Todorov, N. (1999). Calculation of signal detection theory measures. *Behav. Res. Methods Instrum. Comput.* 31, 137–149. doi: 10.3758/BF03207704

Stout, J. C., Busemeyer, J. R., Lin, A., Grant, S. J., and Bonson, K. R. (2004). Cognitive modeling analysis of decision-making processes in cocaine abusers. *Psychon. Bull. Rev.* 11, 742–747. doi: 10.3758/BF03196629

Suhr, J. A., and Tsanadis, J. (2007). Affect and personality correlates of the Iowa gambling task. *Personal. Individ. Differ.* 43, 27–36. doi: 10.1016/j.paid.2006.11.004

Tamir, M., and Robinson, M. D. (2007). The happy spotlight: positive mood and selective attention to rewarding information. *Personal. Soc. Psychol. Bull.* 33, 1124–1136. doi: 10.1177/0146167207301030

Tuvblad, C., Gao, Y., Wang, P., Raine, A., Botwick, T., and Baker, L. A. (2013). The genetic and environmental etiology of decision-making: a longitudinal twin study. *J. Adolesc.* 36, 245–255. doi: 10.1016/j.adolescence.2012.10.006

Tversky, A., and Kahneman, D. (1981). The framing of decisions and the psychology of choice. *Science* 211, 453–458. doi: 10.1126/science.7455683

Tversky, A., and Kahneman, D. (1983). Extensional vs. intuitive reasoning: the conjunction fallacy in probability judgment. *Psychol. Rev.* 90, 293–315. doi: 10.1037/0033-295X.90.4.293

Upton, D. J., Bishara, A. J., Ahn, W.-Y., and Stout, J. C. (2011). Propensity for risk taking and trait impulsivity in the Iowa gambling task. *Personal. Individ. Differ.* 50, 492–495. doi: 10.1016/j.paid.2010.11.013

Von Neumann, J., and Morgenstern, O. (1944). *Theory of games and economic behavior*. Princeton University Press. Princeton.

Wallsten, T. S., Pleskac, T. J., and Lejuez, C. W. (2005). Modeling behavior in a clinically diagnostic sequential risk-taking task. *Psychol. Rev.* 112, 862–880. doi: 10.1037/0033-295X.112.4.862

Waters-Wood, S. M., Xiao, L., Denburg, N. L., Hernandez, M., and Bechara, A. (2012). Failure to learn from repeated mistakes: persistent decision-making impairment as measured by the Iowa gambling task in patients with ventromedial prefrontal cortex lesions. *J. Int. Neuropsychol. Soc.* 18, 927–930. doi: 10.1017/S135561771200063X

Watson, P. A., Gignac, G. E., Weinborn, M., Green, S., and Pestell, C. (2020). A meta-analysis of neuropsychological predictors of outcome following stroke and other non-traumatic acquired brain injuries in adults. *Neuropsychol. Rev.* 30, 194–223. doi: 10.1007/s11065-020-09433-9

Weafer, J., Baggott, M. J., and de Wit, H. (2013). Test-retest reliability of behavioral measures of impulsive choice, impulsive action, and inattention. *Exp. Clin. Psychopharmacol.* 21, 475–481. doi: 10.1037/a0033659

Weber, E. U., and Johnson, E. J. (2009). Mindful judgment and decision making. *Annu. Rev. Psychol.* 60, 53–85. doi: 10.1146/annurev.psych.60.110707.163633

Wood, S. M. W., and Bechara, A. (2014). “The neuroscience of dual (and triple) systems in decision making” in *The neuroscience of risky decision making*. eds. V. F. Reyna and V. Zayas (Washington, DC: American Psychological Association Press)

Xiao, L., Wood, S. M. W., Denburg, N. L., Moreno, G. L., Hernandez, M., and Bechara, A. (2013). Is there a recovery of decision-making function after frontal lobe damage? A study using alternative versions of the Iowa gambling task. *J. Clin. Exp. Neuropsychol.* 35, 518–529. doi: 10.1080/13803395.2013.789484

Yechiam, E., and Busemeyer, J. R. (2008). Evaluating generalizability and parameter consistency in learning models. *Games Econ. Behav.* 63, 370–394. doi: 10.1016/j.geb.2007.08.011

Yechiam, E., Busemeyer, J. R., Stout, J. C., and Bechara, A. (2005). Using cognitive models to map relations between neuropsychological disorders and human decision-making deficits. *Psychol. Sci.* 16, 973–978. doi: 10.1111/j.1467-9280.2005.01646.x

Yechiam, E., and Ert, E. (2011). Risk attitude in decision making: in search of trait-like constructs. *Top. Cogn. Sci.* 3, 166–186. doi: 10.1111/j.1756-8765.2010.01126.x

Frontiers in Psychology

TYPE Mini Review
PUBLISHED 07 December 2023
DOI 10.3389/fpsyg.2023.1265074

The role of emotion in eating behavior and decisions

Oh-Ryeong Ha and Seung-Lark Lim*

Department of Psychology, University of Missouri – Kansas City, Kansas City, MO, United States

EDITED BY
Andrew Kemp,
Swansea University, United Kingdom

REVIEWED BY
Giorgia Varallo,
University of Parma, Italy

*CORRESPONDENCE
Seung-Lark Lim
✉ limse@umkc.edu

RECEIVED 21 July 2023
ACCEPTED 21 November 2023
PUBLISHED 07 December 2023

CITATION
Ha O-R and Lim S-L (2023) The role of emotion in eating behavior and decisions.
Front. Psychol. 14:1265074.
doi: 10.3389/fpsyg.2023.1265074

The present paper aims to provide the latest perspectives and future directions on the association between emotions and eating behavior. We discussed individual differences in the impact of negative emotions on eating, emotional eating as disinhibited eating decisions with heightened reward values of and sensitivity to palatable foods in response to negative emotions and social isolation, in addition to emotional eating as maladaptive coping strategies under negative emotion and stress, hedonic (pleasure-oriented) eating decisions mediated by the brain reward system, and self-controlled (health-oriented) eating decisions mediated by the brain control system. Perspectives on future directions were addressed, including the development of early eating phenotypes in infancy, shared neural mechanisms mediated by the ventromedial prefrontal cortex and the dorsolateral prefrontal cortex in emotion and eating decision regulation, possible roles of interoception incorporating hunger and satiety signals, gut microbiome, the insula and the orbitofrontal cortex, and emotional processing capacities in hedonic eating and weight gain.

KEYWORDS

emotion, negative emotions, emotional eating, hedonic eating, eating behavior, reward values, eating decisions

Introduction

Emotions affect human behavior in various ways, such as motivating goal-directed behaviors, anticipating future outcomes, and supporting reward learning (Dolan, 2002). Emotions also can influence our food consumption and eating decisions regarding how much and when to eat certain foods (Meule and Vogele, 2013). Research has shown that the interplays across different types and intensity of emotions (e.g., negative vs. positive), eating styles (e.g., emotional eating—a tendency to eat in response to negative emotions; restrained eating—cognitive and behavioral restriction of food intake to control body weight; external eating—high susceptibility to food cues that results in craving for high-caloric, palatable foods), weight status, and types of foods (e.g., energy-dense, low-nutritious, unhealthier foods vs. nutritious, healthier foods) lead to different eating behaviors. Yet, emotion-eating mechanisms have not been fully identified. The mechanisms underneath emotion-related changes in eating behavior are multifaceted due to high variabilities across individuals and emotions (Macht, 2008). We focused on current findings exploring the impact of negative emotions on eating behavior and the decision-making mechanism in emotional eating, which provided perspectives on future research directions.

Emotions and their impacts on eating behavior

More often than not, negative emotions tend to decrease food consumption, while positive emotions increase it (Evers et al., 2018; Reichenberger et al., 2018). However, negative emotions can evoke external eating in high-emotional eaters than in low-emotional eaters (Blechert et al., 2014). Negative emotions can increase food consumption in restrained eaters as well due to disturbed cognitive inhibition of food intake (Evers et al., 2018). Furthermore, negative emotions do not necessarily induce increased eating among emotional eaters or individuals with overweight or obese (Evers et al., 2018; Zhou and Tse, 2020).

To explain the inconsistency and varying impacts of negative emotions on eating, recent studies have proposed the importance of individual differences including individualistic emotion-eating experiences and the impact of discrete emotions (Altheimer and Urry, 2019). They emphasized a learned association between discrete negative emotions and eating, rather than general negative emotions, which can vary across individuals (Altheimer and Urry, 2019). People who have previously formed an association between emotion and eating (food consumption or restriction) are more likely to engage in emotional or restricted eating in response to discrete negative emotions like depression and anxiety. For example, sadness increased food consumption more than joy in women high-emotional eaters, while sadness and joy did not differently influence food intake in low-emotional eaters (van Strien et al., 2013). Moreover, depression was related to weight gain regarding body mass index (BMI) change in only women emotional eaters, but not in men emotional eaters as well as external eaters and restricted eaters in either sex (van Strien et al., 2016).

Recent research has elucidated individual differences in how emotions impact hedonic eating (i.e., taste-oriented intake of high-caloric and low-nutrient food with high sugar, salt, and fat for pleasure without hunger) and homeostatic eating (i.e., food intake with a hunger for regulating energy balance) in different contexts (Lutter and Nestler, 2009; Reichenberger et al., 2018; Devonport et al., 2019). Induced anger, fear, and sadness increased consumption of sweet foods (Salerno et al., 2014). But when sensitivity to long-term risks of hedonic eating was primed, sadness restricted hedonic eating, which may be relevant to the function of sadness to become more vigilant to a loss or harm (Salerno et al., 2014).

Both adults' depression and emotional eating were related to hedonic eating and a higher BMI (Konttinen et al., 2010). More severe depressive symptoms were linked to less consumption of fruits and vegetables and more consumption of non-sweet energy-dense foods, but not was not related to more consumption of sweet foods when emotional eating was controlled. When depression was controlled, higher emotional eating was linked to more consumption of sweet and non-sweet energy-dense foods. Results demonstrate that experiencing sadness or depressive moods does not necessarily decrease energy intake. Negative emotions are likely to increase overeating of energy-dense foods and decrease consumption of healthier options. Furthermore, the interaction between negative emotions and emotional eating matters. When emotional eating was examined using ecological momentary assessments (EMA) where people reported their emotions and eating behavior for 10 days, emotional eating and BMI influenced hedonic and homeostatic eating (Reichenberger et al., 2018). High negative emotions increased hedonic eating in high-emotional eaters but decreased it in low-emotional eaters; high negative emotions increased homeostatic eating in people with higher BMI. In addition, emotional processing capabilities may be linked to emotional eating in individuals with obesity. Similar to individuals with anxiety disorders or depression who often demonstrate difficulties in recognizing negative emotions (Demenescu et al., 2010), individuals with obesity are more likely to show difficulties in recognizing fearful and angry facial expressions (Scarpina et al., 2021) and describing and regulating emotions (Fernandes et al., 2018). Challenges in emotional processing may reflect emotional avoidance to cope with negative emotions related to body dissatisfaction or weight stigmatization in individuals with obesity (Fernandes et al., 2018), which could lead to emotional eating.

Findings suggest that emotional eating is prone to unhealthier, taste-oriented food choices under negative emotions. Negative emotions tend to focus on short-term gratification at the expense of long-term health risk considerations. Given the relationship between emotional eating and less adaptive coping strategies like emotion-oriented (i.e., coping through regulating negative emotional responses) and avoidant coping (i.e., avoiding or distracting from negative stress responses) (Spoor et al., 2007), hedonic eating could reflect less adaptive coping attempts for mitigating negative emotions in emotional eaters (Goossens et al., 2009).

Food-evoked emotions, reward values, and food decisions

Food consumption is most likely to elicit positive emotions like satisfaction and enjoyment rather than negative emotions (Desmet and Schifferstein, 2008). Conceptually, people associate sweet taste with positive emotion-laden words like happiness, love, grateful, acceptance, hug, and kiss, and bitter taste with negative emotion-laden words like sad, disgust, and rejection (Zhou and Tse, 2020). Sensory experiences can be embodied in psychological states and emotions through repeated associations between taste and emotion (e.g., associations between sweet taste and happiness) from early on in our lives (Zhou and Tse, 2020, 2022).

Individualistic food experiences from prenatal periods may impact sensory preferences. Infants are predisposed to like sweet and salty tastes and dislike sour and bitter tastes (Birch and Fisher, 1998). It has adaptive values that allow infants to find safe food sources like the sweet taste of breast milk. However, in the most modern obesogenic societies of food abundance, a preference for sweet, salty, and fatty foods is more likely to result in poorer nutritious choices and weight gain (Birch and Fisher, 1998). Developing less predisposed-taste-oriented food choices can be critical for physical and mental health. Accepting more nutritious foods (e.g., leafy vegetables and beans) and learning to regulate emotions adaptively could prevent disinhibited overconsumption of sweet, high-caloric, low-nutritious foods in response to negative emotions and stress. Nevertheless, challenges lie in that we are inclined to "eat" palatable and energy-dense foods rather than reject foods for secure energy intake (Ha et al., 2016). Anticipating and consuming palatable foods are associated with pleasure mediated by the brain reward system (Kringelbach et al., 2012; Berridge and Kringelbach, 2013; Volkow et al., 2013; Alonso-Alonso et al., 2015). Moreover, food taste preference is a major determinant of eating decisions (Raghunathan et al., 2006; Gutjar et al., 2015; Ha et al., 2019).

People make eating decisions based on subjective reward values of food attributes, specifically, food taste and health. Decision values of food taste and health attributes are encoded in the ventromedial prefrontal cortex (vmPFC) that involved in reward value computation (Hare et al., 2009; Clithero and Rangel, 2013; Bruce et al., 2016; Lim et al., 2023). Hedonic, pleasure-oriented decisions that predominantly incorporate food taste attributes lead to less nutritious, unhealthier eating and/or weight gain (Lim et al., 2018, 2023). To make more nutritious, healthier decisions, the health attributes of food need to be considered. In health-oriented, self-controlled decisions (i.e., refusing tasty but unhealthy foods or eating not-tasty but healthy foods) mediated by the brain control system (Chib et al., 2009; Hare et al., 2009; Lim et al., 2016, 2023), food health attributes are incorporated early and significant enough during decision process (Sullivan et al., 2015; Lim et al., 2018), which allows people to pursue long-term health benefits rather than immediate pleasure from palatable, but less nutritious and unhealthier foods (Ha et al., 2016, 2021; van Meer et al., 2016; Lim et al., 2018).

Emotional eating is related to impulsive, less self-controlled decisions in response to negative emotions or stress (Elfhag and Morey, 2008; Verstuyf et al., 2013; Zhu et al., 2014). Emotional eating tends to be associated with external eating (e.g., overconsumption in response to external food cues like the smell of food and food advertisements) (van Bloemendaal et al., 2015; van Strien, 2018), which supports lapses of self-control in emotional eating. Overriding immediate pleasure for long-term health goals becomes arduous for emotional eaters when emotional distress increases reward values of palatable, high-caloric foods and sensitivity to those food cues in the brain reward system including the orbitofrontal cortex (OFC) and ventral striatum (Wagner et al., 2012; van Bloemendaal et al., 2015). Under negative emotions or stress, heightened sensitivity to food cues and reward values lead to increased cravings for palatable foods and disinhibited eating in people with obesity as well (Jastreboff et al., 2013). Craving, or motivations for seeking palatable foods are encoded in the mesolimbic dopamine reward system, especially in the substantia nigra (SN) and ventral tegmental area (VTA) (Meye and Adan, 2014). Intranasal oxytocin administration reduces the consumption of palatable foods and decreases activations in the VTA in response to high-calorie food cues in men with overweight and obesity (Plessow et al., 2018). These findings suggest that associations between negative emotion and hedonic eating are linked to changes in the brain reward system, which make people more prone to craving and overconsumption of palatable foods, especially among emotional eaters and people with excessive weight.

Hedonic eating is also linked to affection and social needs. Sweet taste often forms an association with warmth and love (Chan et al., 2013; Ren et al., 2015). Sweet taste and a romantic partner activate similar neural responses in the anterior cingulate cortex that are involved in the reward system (Bartels and Zeki, 2000; Araujo et al., 2003). When people are lacking warmth and love, deprivation of positive emotions and social connection could result in compensatory reward-seeking behaviors, including craving and over-consumption of low-nutritious sweet foods (Henriksen et al., 2014; Tomova et al., 2020; Doan et al., 2022). Loneliness increased craving for sugar-sweetened beverages measured using an EMA in adolescents (Doan et al., 2022). Loneliness increased the consumption of sweet beverages, while perceived social connection decreased the consumption of sweet beverages in pregnant women (Henriksen et al., 2014). In young adults, deprivation of social connection and food evoked similar behavioral and neural responses (Tomova et al., 2020). Acute social isolation resulted in increased negative emotions and increased social craving, and fasting resulted in increased negative emotions and increased food craving and hunger (Tomova et al., 2020). The level of self-reported cravings for social connection and cravings for food after deprivation were strongly correlated. Further, both types of deprivation evoked similar responses in dopaminergic midbrain regions involved in craving and seeking palatable foods, specifically in the SN and VTA.

In sum, food evokes positive emotions. Learned associations between food and negative emotions may heighten emotional eating that is prone to disinhibited eating decisions of seeking palatable foods in response to negative emotions, social isolation, and stress. For better mental and physical health, it will be crucial to develop more adaptive emotion regulation, coping strategies, and health-oriented, self-controlled eating decisions.

Discussion

While much is yet to unfold, recent advances may shed light on new perspectives in understanding the relationship between emotion and eating behaviors.

Exploring pleasure-seeking and eating phenotypes in early life may provide important knowledge about the development of hedonic eating. Food preferences and appetite traits begin to develop from prenatal periods influenced by genetic predispositions and maternal food choices (Ventura and Worobey, 2013). Given that infants transition to adult foods during the first 2 years (Carruth et al., 2004), early food experiences could lay the foundation for food preferences (Domel et al., 1996; Gibson et al., 1998; Howard et al., 2012; Mura Paroche et al., 2017). One of the prominent obesogenic eating phenotypes is sensitivity to external food cues, which often results in overeating that potentially leads to obesity (Carnell et al., 2013). One study demonstrated that 6- to 12-month-olds with rapid weight gain showed higher responsivity (touching) to foods over nonfoods, suggesting that early heightened sensitivity to food cues could influence rapid weight gain (Buvinger et al., 2017). Moreover, 9- to 18-month-old infants with more rapid weight gain (i.e., greater weight-for-length z scores) found a favorite food was more rewarding than nonfood alternatives (a toy and DVD) compared to lean infants. Interestingly, reward values of nonfood alternatives were significantly lower among infants with more rapid weight gain than lean infants. These findings suggest that infants with rapid weight gain have developed heightened food reward-seeking along with a lack of alternative sources for pleasure-seeking, which could contribute to hedonic eating and weight gain in their later lives. It will be worth examining how early preferences to food and other objects are associated with the development of hedonic eating and risks for obesity.

A more holistic understanding of shared neural mechanisms of emotion and eating behavior may shed light on the intervention of hedonic eating. Common neural mechanisms of emotion and eating behavior regulations have been identified (Godet et al., 2022). The vmPFC mediates valuations of emotional food stimuli considering people's current goals and contexts (Ochsner et al., 2012; Lim et al., 2023). The dorsolateral prefrontal cortex (dlPFC) mediates both emotion regulations (Ochsner and Gross, 2005; Ochsner et al., 2012) and eating regulations (Hare et al., 2009; Hutcherson et al., 2012) by incorporating long-term goals into value representation in the vmPFC (Hare et al., 2009; Hutcherson et al., 2012). Recent research has demonstrated the positive effect of the dlPFC modification using transcranial direct-current stimulation (tDCS) on emotion, such as reduced emotional reactivity to negative emotions (Clarke et al., 2020), enhanced cognitive control of emotion regulation (Feeser et al., 2014), and decreased anxiety and stress responses measured by cortisol levels (Mehrsafar et al., 2020). Similarly, some research demonstrated that the dlPFC modulation using tDCS reduced food craving, liking, and/or consumption in healthy-weight adults with higher food craving (Jauch-Chara et al., 2014; Kekic et al., 2014; Lapenta et al., 2014; Anderson et al., 2023), in adults with overweight and higher food craving (Ljubisavljevic et al., 2016), and adults with obesity and binge eating disorder (Burgess et al., 2016). However, other studies did not find significant changes in food cravings, choice, and consumption (Georgii et al., 2017; Ray et al., 2017; Beaumont et al., 2021). Individual differences in eating and psychological aspects could play a role in inconsistent findings, given results vary depending on the level of susceptibility to hedonic eating, types of eating behaviors, and psychological traits (Ray et al., 2017). For example, the dlPFC modulation via tDCS did not change food cravings and consumption in healthy-weight adults with lower hedonic eating (Beaumont et al., 2021). The dlPFC modulation reduced food liking (pleasure) but not unhealthy food choices in healthy-weight adults with higher food cravings (Anderson et al., 2023). Further research is necessary to determine the effectiveness of neural modulation in food craving and consumption.

Recently, individual differences in interoception and gut microbiome have been considered to provide an insight of the association between emotion and eating. Interoception is the ability to accurately sense internal body signals (Garfinkel et al., 2015; Khalsa et al., 2018). Poorer interoception is linked to worse emotion regulation (Füstös et al., 2012), higher emotional eating and BMI (Robinson et al., 2021), and disordered eating (Ahlich and Rancourt, 2022). Hypersensitivity to interoceptive hunger signals and less accurate detection of satiety and energy balance signals are prone to hedonic eating and obesity (Simmons and DeVille, 2017). The variation in gut microbiome consisted of 10^{13} to 10^{14} microorganisms inhabiting the gastrointestinal system (Le Chatelier et al., 2013) including reduced bacterial diversity and altered composition may contribute to delayed satiety setpoint (Yatsunenko et al., 2012), food craving (Alcock et al., 2014), dysregulated energy balance and weight gain (Le Chatelier et al., 2013; Davis, 2016; Torres-Fuentes et al., 2017), and disordered eating (Terry et al., 2022). Via the vagus nerve, some gut microbiota and gastrointestinal signals are delivered to the brain, which bidirectionally influence emotional experiences like anxiety and stress (Breit et al., 2018). The insula integrates projected interoceptive signals with emotional, cognitive, and motivational signals that result in explicit experiences of positive and negative emotions (Namkung et al., 2017). The anterior insula relays saliency signals associated with emotions (e.g., pleasure, pain) to dlPFC for initiating attentive control (Menon and Uddin, 2010) and represents past emotional experiences in similar contexts to vmPFC to evaluate outcomes for future decisions (Namkung et al., 2017). The anterior insula is a part of the primary taste and olfactory cortex (Rolls, 2016), along with the OFC involved in the modulation of taste reactions, affective representation of rewards (e.g., pleasure from palatable foods), and food-evoked emotion (Kringelbach, 2005). Research reported that higher emotional eating was linked to greater activations of the insula and the OFC (Bohon et al., 2009; van Bloemendaal et al., 2015) but see Bohon (2014). These findings may account for the multifaceted role of the insula and the OFC across interoception, emotion generation and modulation, taste perception, and responses to food cues, which suggests overlapping mechanisms under emotion and food processing (Frank et al., 2013).

Altogether, we have addressed commonalities across emotion and eating, while emphasizing the importance of variability and individual differences in understanding the association between emotion and eating behaviors. Further investigations on neural, physiological, and decision-making mechanisms of emotional eating and effective intervention and prevention of hedonic and emotional eating are warranted.

Author contributions

O-RH: Writing – original draft, Writing – review & editing. S-LL: Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was supported by the Noble Fund Award to S-LL.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Ahlich, E., and Rancourt, D. (2022). Boredom proneness, interoception, and emotional eating. *Appetite* 178:106167. doi: 10.1016/j.appet.2022.106167

Alcock, J., Maley, C. C., and Aktipis, C. A. (2014). Is eating behavior manipulated by the gastrointestinal microbiota? Evolutionary pressures and potential mechanisms. *Bioessays* 36, 940–949. doi: 10.1002/bies.201400071

Alonso-Alonso, M., Woods, S. C., Pelchat, M., Grigson, P. S., Stice, E., Farooqi, S., et al. (2015). Food reward system: current perspectives and future research needs. *Nutr. Rev.* 73, 296–307. doi: 10.1093/nutrit/nuv002

Altheimer, G., and Urry, H. L. (2019). Do emotions cause eating? The role of previous experiences and social context in emotional eating. *Curr. Dir. Psychol. Sci.* 28, 234–240. doi: 10.1177/0963721419837685

Anderson, E. C., Cantelon, J. A., Holmes, A., Giles, G. E., Brunyé, T. T., and Kanarek, R. (2023). Transcranial direct current stimulation (tDCS) to dorsolateral prefrontal cortex influences perceived pleasantness of food. *Heliyon* 9:e13275. doi: 10.1016/j.heliyon.2023.e13275

Araujo, I. E. T., Kringelbach, M. L., Rolls, E. T., and Hobden, P. (2003). Representation of umami taste in the human brain. *J. Neurophysiol.* 90, 313–319. doi: 10.1152/jn.00669.2002

Bartels, A., and Zeki, S. (2000). The neural basis of romantic love. *Neuroreport* 11, 3829–3834. doi: 10.1097/00001756-200011270-00046

Beaumont, J. D., Davis, D., Dalton, M., Nowicky, A., Russell, M., and Barwood, M. J. (2021). The effect of transcranial direct current stimulation (tDCS) on food craving, reward and appetite in a healthy population. *Appetite* 157:105004. doi: 10.1016/j.appet.2020.105004

Berridge, K. C., and Kringelbach, M. L. (2013). Neuroscience of affect: brain mechanisms of pleasure and displeasure. *Curr. Opin. Neurobiol.* 23, 294–303. doi: 10.1016/j.conb.2013.01.017

Birch, L. L., and Fisher, J. O. (1998). Development of eating behaviors among children and adolescents. *Pediatrics* 101, 539–549. doi: 10.1542/peds.101.S2.539

Blechert, J., Goltsche, J. E., Herbert, B. M., and Wilhelm, F. H. (2014). Eat your troubles away: electrocortical and experiential correlates of food image processing are related to emotional eating style and emotional state. *Biol. Psychol.* 96, 94–101. doi: 10.1016/j.biopsycho.2013.12.007

Bohon, C. (2014). Greater emotional eating scores associated with reduced frontolimbic activation to palatable taste in adolescents. *Obesity (Silver Spring)* 22, 1814–1820. doi: 10.1002/oby.20759

Bohon, C., Stice, E., and Spoor, S. (2009). Female emotional eaters show abnormalities in consummatory and anticipatory food reward: a functional magnetic resonance imaging study. *Int. J. Eat. Disord.* 42, 210–221. doi: 10.1002/eat.20615

Breit, S., Kupferberg, A., Rogler, G., and Hasler, G. (2018). Vagus nerve as modulator of the brain-gut Axis in psychiatric and inflammatory disorders. *Front. Psych.* 9:44. doi: 10.3389/fpsyt.2018.00044

Bruce, A. S., Pruitt, S. W., Ha, O. R., Cherry, J. B., Smith, T. R., Bruce, J. M., et al. (2016). The influence of televised food commercials on Children's food choices: evidence from ventromedial prefrontal cortex activations. *J. Pediatr.* 177:27–32 e21. doi: 10.1016/j.jpeds.2016.06.067

Burgess, E. E., Sylvester, M. D., Morse, K. E., Amthor, F. R., Mrug, S., Lokken, K. L., et al. (2016). Effects of transcranial direct current stimulation (tDCS) on binge-eating disorder. *Int. J. Eat. Disord.* 49, 930–936. doi: 10.1002/eat.22554

Buvinger, E., Rosenblum, K., Miller, A. L., Kaciroti, N. A., and Lumeng, J. C. (2017). Observed infant food cue responsivity: associations with maternal report of infant eating behavior, breastfeeding, and infant weight gain. *Appetite* 112, 219–226. doi: 10.1016/j.appet.2017.02.002

Carnell, S., Benson, L., Pryor, K., and Driggin, E. (2013). Appetitive traits from infancy to adolescence: using behavioral and neural measures to investigate obesity risk. *Physiol. Behav.* 121, 79–88. doi: 10.1016/j.physbeh.2013.02.015

Carruth, B. R., Ziegler, P. J., Gordon, A., and Barr, S. I. (2004). Prevalence of picky eaters among infants and toddlers and their caregivers' decisions about offering a new food. *J. Am. Diet. Assoc.* 104, s57–s64. doi: 10.1016/j.jada.2003.10.024

Chan, K. Q., Tong, E. M. W., Tan, D. H., and Koh, A. H. Q. (2013). What do love and jealousy taste like? *Emotion* 13, 1142–1149. doi: 10.1037/a0033758

Chib, V. S., Rangel, A., Shimojo, S., and O'Doherty, J. P. (2009). Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. *J. Neurosci.* 29, 12315–12320. doi: 10.1523/jneurosci.2575-09.2009

Clarke, P. J. F., Van Bockstaele, B., Marinovic, W., Howell, J. A., Boyes, M. E., and Notebaert, L. (2020). The effects of left DLPFC tDCS on emotion regulation, biased attention, and emotional reactivity to negative content. *Cogn. Affect. Behav. Neurosci.* 20, 1323–1335. doi: 10.3758/s13415-020-00840-2

Clithero, J. A., and Rangel, A. (2013). Informatic parcellation of the network involved in the computation of subjective value. *Soc. Cogn. Affect. Neurosci.* 9, 1289–1302. doi: 10.1093/scan/nst106

Davis, C. D. (2016). The gut microbiome and its role in obesity. *Nutr. Today* 51, 167–174. doi: 10.1097/nt.0000000000000167

Demenescu, L. R., Kortekaas, R., den Boer, J. A., and Aleman, A. (2010). Impaired attribution of emotion to facial expressions in anxiety and major depression. *PLoS One* 5:e15058. doi: 10.1371/journal.pone.0015058

Desmet, P. M., and Schifferstein, H. N. (2008). Sources of positive and negative emotions in food experience. *Appetite* 50, 290–301. doi: 10.1016/j.appet.2007.08.003

Devonport, T. J., Nicholls, W., and Fullerton, C. (2019). A systematic review of the association between emotions and eating behaviour in normal and overweight adult populations. *J. Health Psychol.* 24, 3–24. doi: 10.1177/1359105317697813

Doan, S. N., Xie, B., Zhou, Y., Lei, X., and Reynolds, K. D. (2022). Loneliness and cravings for sugar-sweetened beverages among adolescents. *Pediatr. Obes.* 17:e12834. doi: 10.1111/ijpo.12834

Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science* 298, 1191–1194. doi: 10.1126/science.1076358

Domel, S., Thompson, W., Davis, H., Baranowski, T., Leonard, S., and Baranowski, J. (1996). Psychosocial predictors of fruit and vegetable consumption among elementary school children. *Health Educ. Res.* 11, 299–308. doi: 10.1093/her/11.3.299

Elfhag, K., and Morey, L. C. (2008). Personality traits and eating behavior in the obese: poor self-control in emotional and external eating but personality assets in restrained eating. *Eat. Behav.* 9, 285–293. doi: 10.1016/j.eatbeh.2007.10.003

Evers, C., Dingemans, A., Junghans, A. F., and Boeve, A. (2018). Feeling bad or feeling good, does emotion affect your consumption of food? A meta-analysis of the experimental evidence. *Neurosci. Biobehav. Rev.* 92, 195–208. doi: 10.1016/j.neubiorev.2018.05.028

Feeser, M., Prehn, K., Kazzer, P., Mungee, A., and Bajbouj, M. (2014). Transcranial direct current stimulation enhances cognitive control during emotion regulation. *Brain Stimul.* 7, 105–112. doi: 10.1016/j.brs.2013.08.006

Fernandes, J., Ferreira-Santos, F., Miller, K., and Torres, S. (2018). Emotional processing in obesity: a systematic review and exploratory meta-analysis. *Obes. Rev.* 19, 111–120. doi: 10.1111/obr.12607

Frank, S., Kullmann, S., and Veit, R. (2013). Food related processes in the insular cortex. *Front. Hum. Neurosci.* 7:499. doi: 10.3389/fnhum.2013.00499

Füstös, J., Gramann, K., Herbert, B. M., and Pollatos, O. (2012). On the embodiment of emotion regulation: interoceptive awareness facilitates reappraisal. *Soc. Cogn. Affect. Neurosci.* 8, 911–917. doi: 10.1093/scan/nss089

Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., and Critchley, H. D. (2015). Knowing your own heart: distinguishing interoceptive accuracy from interoceptive awareness. *Biol. Psychol.* 104, 65–74. doi: 10.1016/j.biopsycho.2014.11.004

Georgii, C., Goldhofer, P., Meule, A., Richard, A., and Blechert, J. (2017). Food craving, food choice and consumption: the role of impulsivity and sham-controlled tDCS stimulation of the right dlPFC. *Physiol. Behav.* 177, 20–26. doi: 10.1016/j.physbeh.2017.04.004

Gibson, R. S., Ferguson, E. L., and Lehrfeld, J. (1998). Complementary foods for infant feeding in developing countries: their nutrient adequacy and improvement. *Eur. J. Clin. Nutr.* 52, 764–770. doi: 10.1038/sj.ejcn.1600645

Godet, A., Fortier, A., Bannier, E., Coquery, N., and Val-Laillet, D. (2022). Interactions between emotions and eating behaviors: Main issues, neuroimaging contributions, and innovative preventive or corrective strategies. *Rev. Endocrine Metab. Disord.* 23, 807–831. doi: 10.1007/s11154-021-09700-x

Goossens, L., Braet, C., Van Vlierberghe, L., and Mels, S. (2009). Loss of control over eating in overweight youngsters: the role of anxiety, depression and emotional eating. *Eur. Eat. Disord. Rev.* 17, 68–78. doi: 10.1002/erv.892

Gutjar, S., Dalenberg, J. R., de Graaf, C., de Wijk, R. A., Palascha, A., Renken, R. J., et al. (2015). What reported food-evoked emotions may add: a model to predict consumer food choice. *Food Qual. Prefer.* 45, 140–148. doi: 10.1016/j.foodqual.2015.06.008

Ha, O. R., Bruce, A. S., Killian, H. J., Davis, A. M., and Lim, S. L. (2021). Shared dynamics of food decision-making in mother-child dyads. *Front. Psychol.* 12:695388. doi: 10.3389/fpsyg.2021.695388

Ha, O. R., Bruce, A. S., Pruitt, S. W., Cherry, J. B., Smith, T. R., Burkart, D., et al. (2016). Healthy eating decisions require efficient dietary self-control in children: a mouse-tracking food decision study. *Appetite* 105, 575–581. doi: 10.1016/j.appet.2016.06.027

Ha, O. R., Lim, S. L., Bruce, J. M., and Bruce, A. S. (2019). Unhealthy foods taste better among children with lower self-control. *Appetite* 139, 84–89. doi: 10.1016/j.appet.2019.04.015

Hare, T. A., Camerer, C. F., and Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. *Science* 324, 646–648. doi: 10.1126/science.1168450

Henriksen, R. E., Torsheim, T., and Thuen, F. (2014). Loneliness, social integration and consumption of sugar-containing beverages: testing the social baseline theory. *PLoS One* 9:e104421. doi: 10.1371/journal.pone.0104421

Howard, A. J., Mallan, K. M., Byrne, R., Magarey, A., and Daniels, L. A. (2012). Toddlers' food preferences. The impact of novel food exposure, maternal preferences and food neophobia. *Appetite* 59, 818–825. doi: 10.1016/j.appet.2012.08.022

Hutcherson, C. A., Plassmann, H., Gross, J. J., and Rangel, A. (2012). Cognitive regulation during decision making shifts behavioral control between ventromedial and dorsolateral prefrontal value systems. *J. Neurosci.* 32, 13543–13554. doi: 10.1523/jneurosci.6387-11.2012

Jastreboff, A. M., Sinha, R., Lacadie, C., Small, D. M., Sherwin, R. S., and Potenza, M. N. (2013). Neural correlates of stress- and food cue–induced food craving in obesity: association with insulin levels. *Diabetes Care* 36, 394–402. doi: 10.2337/dc12-1112

Jauch-Chara, K., Kistenmacher, A., Herzog, N., Schwarz, M., Schweiger, U., and Oltmanns, K. M. (2014). Repetitive electric brain stimulation reduces food intake in humans. *Am. J. Clin. Nutr.* 100, 1003–1009. doi: 10.3945/ajcn.113.075481

Kekic, M., McClelland, J., Campbell, I., Nestler, S., Rubia, K., David, A. S., et al. (2014). The effects of prefrontal cortex transcranial direct current stimulation (tDCS) on food craving and temporal discounting in women with frequent food cravings. *Appetite* 78, 55–62. doi: 10.1016/j.appet.2014.03.010

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., et al. (2018). Interoception and mental health: a roadmap. *Biol. Psychiatry Cogn. Neurosci. Neuroimaging* 3, 501–513. doi: 10.1016/j.bpsc.2017.12.004

Konttinen, H., Mannisto, S., Sarlio-Lahteenkorva, S., Silventoinen, K., and Haukkala, A. (2010). Emotional eating, depressive symptoms and self-reported food consumption. A population-based study. *Appetite* 54, 473–479. doi: 10.1016/j.appet.2010.01.014

Kringelbach, M. L. (2005). The human orbitofrontal cortex: linking reward to hedonic experience. *Nat. Rev. Neurosci.* 6, 691–702. doi: 10.1038/nrn1747

Kringelbach, M. L., Stein, A., and van Hartevelt, T. J. (2012). The functional human neuroanatomy of food pleasure cycles. *Physiol. Behav.* 106, 307–316. doi: 10.1016/j.physbeh.2012.03.023

Lapenta, O. M., Sierve, K. D., de Macedo, E. C., Fregni, F., and Boggio, P. S. (2014). Transcranial direct current stimulation modulates ERP-indexed inhibitory control and reduces food consumption. *Appetite* 83, 42–48. doi: 10.1016/j.appet.2014.08.005

Le Chatelier, E., Nielsen, T., Qin, J., Prifti, E., Hildebrand, F., Falony, G., et al. (2013). Richness of human gut microbiome correlates with metabolic markers. *Nature* 500, 541–546. doi: 10.1038/nature12506

Lim, S. L., Bruce, A. S., and Shook, R. P. (2023). Neurocomputational mechanisms of food and physical activity decision-making in male adolescents. *Sci. Rep.* 13:6145. doi: 10.1038/s41598-023-32823-x

Lim, S. L., Cherry, J. B., Davis, A. M., Balakrishnan, S. N., Ha, O. R., Bruce, J. M., et al. (2016). The child brain computes and utilizes internalized maternal choices. *Nat. Commun.* 7:11700. doi: 10.1038/ncomms11700

Lim, S. L., Penrod, M. T., Ha, O. R., Bruce, J. M., and Bruce, A. S. (2018). Calorie labeling promotes dietary self-control by shifting the temporal dynamics of health- and taste-attribute integration in overweight individuals. *Psychol. Sci.* 29, 447–462. doi: 10.1177/0956797617737871

Ljubisavljevic, M., Maxood, K., Bjekic, J., Oommen, J., and Nagelkerke, N. (2016). Long-term effects of repeated prefrontal cortex transcranial direct current stimulation (tDCS) on food craving in Normal and overweight young adults. *Brain Stimul.* 9, 826–833. doi: 10.1016/j.brs.2016.07.002

Lutter, M., and Nestler, E. J. (2009). Homeostatic and hedonic signals interact in the regulation of food intake. *J. Nutr.* 139, 629–632. doi: 10.3945/jn.108.097618

Macht, M. (2008). How emotions affect eating: a five-way model. *Appetite* 50, 1–11. doi: 10.1016/j.appet.2007.07.002

Mehrsafar, A. H., Rosa, M. A. S., Zadeh, A. M., and Gazerani, P. (2020). A feasibility study of application and potential effects of a single session transcranial direct current stimulation (tDCS) on competitive anxiety, mood state, salivary levels of cortisol and alpha amylase in elite athletes under a real-world competition. *Physiol. Behav.* 227:113173. doi: 10.1016/j.physbeh.2020.113173

Menon, V., and Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Struct. Funct.* 214, 655–667. doi: 10.1007/s00429-010-0262-0

Meule, A., and Vogele, C. (2013). The psychology of eating. *Front. Psychol.* 4:215. doi: 10.3389/fpsyg.2013.00215

Meye, F. J., and Adan, R. A. (2014). Feelings about food: the ventral tegmental area in food reward and emotional eating. *Trends Pharmacol. Sci.* 35, 31–40. doi: 10.1016/j.tips.2013.11.003

Mura Paroche, M., Caton, S. J., Vereijken, C. M., Weenen, H., and Houston-Price, C. (2017). How infants and young children learn about food: a systematic review. *Front. Psychol.* 8:1046. doi: 10.3389/fpsyg.2017.01046

Namkung, H., Kim, S. H., and Sawa, A. (2017). The insula: an underestimated brain area in clinical neuroscience, psychiatry, and neurology. *Trends Neurosci.* 40, 200–207. doi: 10.1016/j.tins.2017.02.002

Ochsner, K. N., and Gross, J. J. (2005). The cognitive control of emotion. *Trends Cogn. Sci.* 9, 242–249. doi: 10.1016/j.tics.2005.03.010

Ochsner, K. N., Silvers, J. A., and Buhle, J. T. (2012). Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. *Ann. N. Y. Acad. Sci.* 1251, E1–E24. doi: 10.1111/j.1749-6632.2012.06751.x

Plessow, F., Marengi, D. A., Perry, S. K., Felicione, J. M., Franklin, R., Holmes, T. M., et al. (2018). Effects of intranasal oxytocin on the blood oxygenation level-dependent signal in food motivation and cognitive control pathways in overweight and obese men. *Neuropsychopharmacology* 43, 638–645. doi: 10.1038/npp.2017.226

Raghunathan, R., Naylor, R. W., and Hoyer, W. D. (2006). The unhealthy= tasty intuition and its effects on taste inferences, enjoyment, and choice of food products. *J. Mark.* 70, 170–184. doi: 10.1509/jmkg.70.4.170

Ray, M. K., Sylvester, M. D., Osborn, L., Helms, J., Turan, B., Burgess, E. E., et al. (2017). The critical role of cognitive-based trait differences in transcranial direct current stimulation (tDCS) suppression of food craving and eating in frank obesity. *Appetite* 116, 568–574. doi: 10.1016/j.appet.2017.05.046

Reichenberger, J., Kuppens, P., Liedlgruber, M., Wilhelm, F. H., Tiefengrabner, M., Ginzinger, S., et al. (2018). No haste, more taste: an EMA study of the effects of stress, negative and positive emotions on eating behavior. *Biol. Psychol.* 131, 54–62. doi: 10.1016/j.biopsycho.2016.09.002

Ren, D., Tan, K., Arriaga, X. B., and Chan, K. Q. (2015). Sweet love:the effects of sweet taste experience on romantic perceptions. *J. Soc. Pers. Relat.* 32, 905–921. doi: 10.1177/0265407514554512

Robinson, E., Marty, L., Higgs, S., and Jones, A. (2021). Interoception, eating behaviour and body weight. *Physiol. Behav.* 237:113434. doi: 10.1016/j.physbeh.2021.113434

Rolls, E. T. (2016). Functions of the anterior insula in taste, autonomic, and related functions. *Brain Cogn.* 110, 4–19. doi: 10.1016/j.bandc.2015.07.002

Salerno, A., Laran, J., and Janiszewski, C. (2014). Hedonic eating goals and emotion: when sadness decreases the desire to indulge. *J. Consum. Res.* 41, 135–151. doi: 10.1086/675299

Scarpina, F., Varallo, G., Castelnuovo, G., Capodaglio, P., Molinari, E., and Mauro, A. (2021). Implicit facial emotion recognition of fear and anger in obesity. *Eat. Weight Disord.* 26, 1243–1251. doi: 10.1007/s40519-020-01010-6

Simmons, W. K., and DeVille, D. C. (2017). Interoceptive contributions to healthy eating and obesity. *Curr. Opin. Psychol.* 17, 106–112. doi: 10.1016/j.copsyc.2017.07.001

Spoor, S. T., Bekker, M. H., Van Strien, T., and van Heck, G. L. (2007). Relations between negative affect, coping, and emotional eating. *Appetite* 48, 368–376. doi: 10.1016/j.appet.2006.10.005

Sullivan, N., Hutcherson, C., Harris, A., and Rangel, A. (2015). Dietary self-control is related to the speed with which attributes of healthfulness and tastiness are processed [research support, N.I.H., extramural research support, non-U.S. Gov't research support, U.S. Gov't, non-P.H.S.]. *Psychol. Sci.* 26, 122–134. doi: 10.1177/0956797614559543

Terry, S. M., Barnett, J. A., and Gibson, D. L. (2022). A critical analysis of eating disorders and the gut microbiome. *J. Eat. Disord.* 10:154. doi: 10.1186/s40337-022-00681-z

Tomova, L., Wang, K. L., Thompson, T., Matthews, G. A., Takahashi, A., Tye, K. M., et al. (2020). Acute social isolation evokes midbrain craving responses similar to hunger. *Nat. Neurosci.* 23, 1597–1605. doi: 10.1038/s41593-020-00742-z

Torres-Fuentes, C., Schellekens, H., Dinan, T. G., and Cryan, J. F. (2017). The microbiota–gut–brain axis in obesity. *Lancet Gastroenterol. Hepatol.* 2, 747–756. doi: 10.1016/S2468-1253(17)30147-4

van Bloemendaal, L., Veltman, D. J., ten Kulve, J. S., Drent, M. L., Barkhof, F., Diamant, M., et al. (2015). Emotional eating is associated with increased brain responses to food-cues and reduced sensitivity to GLP-1 receptor activation. *Obesity (Silver Spring)* 23, 2075–2082. doi: 10.1002/oby.21200

van Meer, F., Charbonnier, L., and Smeets, P. A. M. (2016). Food decision-making: effects of weight status and age. *Curr. Diab. Rep.* 16:84. doi: 10.1007/s11892-016-0773-z

van Strien, T. (2018). Causes of emotional eating and matched treatment of obesity. *Curr. Diab. Rep.* 18:35. doi: 10.1007/s11892-018-1000-x

van Strien, T., Cebolla, A., Etchemendy, E., Gutierrez-Maldonado, J., Ferrer-Garcia, M., Botella, C., et al. (2013). Emotional eating and food intake after sadness and joy. *Appetite* 66, 20–25. doi: 10.1016/j.appet.2013.02.016

van Strien, T., Konttinen, H., Homberg, J. R., Engels, R. C., and Winkens, L. H. (2016). Emotional eating as a mediator between depression and weight gain. *Appetite* 100, 216–224. doi: 10.1016/j.appet.2016.02.034

Ventura, A. K., and Worobey, J. (2013). Early influences on the development of food preferences. *Curr. Biol.* 23, R401–R408. doi: 10.1016/j.cub.2013.02.037

Verstuyf, J., Vansteenkiste, M., Soenens, B., Boone, L., and Mouratidis, A. (2013). Daily ups and downs in Women's binge eating symptoms: the role of basic psychological needs, general self-control, and emotional eating. *J. Soc. Clin. Psychol.* 32, 335–361. doi: 10.1521/jscp.2013.32.3.335

Volkow, N. D., Wang, G.-J., Tomasi, D., and Baler, R. D. (2013). Obesity and addiction: neurobiological overlaps. *Obes. Rev.* 14, 2–18. doi: 10.1111/j.1467-789X.2012.01031.x

Wagner, D. D., Boswell, R. G., Kelley, W. M., and Heatherton, T. F. (2012). Inducing negative affect increases the reward value of appetizing foods in dieters. *J. Cogn. Neurosci.* 24, 1625–1633. doi: 10.1162/jocn_a_00238

Yatsunenko, T., Rey, F. E., Manary, M. J., Trehan, I., Dominguez-Bello, M. G., Contreras, M., et al. (2012). Human gut microbiome viewed across age and geography. *Nature* 486, 222–227. doi: 10.1038/nature11053

Zhou, Y., and Tse, C.-S. (2020). The taste of emotion: metaphoric association between taste words and emotion/emotion-laden words. *Front. Psychol.* 11:986. doi: 10.3389/fpsyg.2020.00986

Zhou, Y., and Tse, C.-S. (2022). Sweet taste brings happiness, but happiness does not taste sweet: the unidirectionality of taste-emotion metaphoric association. *J. Cogn. Psychol.* 34, 339–361. doi: 10.1080/20445911.2021.2020797

Zhu, H., Luo, X., Cai, T., Li, Z., and Liu, W. (2014). Self-control and parental control mediate the relationship between negative emotions and emotional eating among adolescents. *Appetite* 82, 202–207. doi: 10.1016/j.appet.2014.06.106

frontiers | Frontiers in Psychology

TYPE Original Research
PUBLISHED 07 February 2024
DOI 10.3389/fpsyg.2024.1322792

Sustained training with novel distractors attenuates the behavioral interference of emotional pictures but does not affect the electrocortical markers of emotional processing

Vera Ferrari[1], Francesca Canturi[1], Andrea De Cesarei[2] and Maurizio Codispoti[2]*

[1]Department of Medicine and Surgery, University of Parma, Parma, Italy, [2]Department of Psychology, University of Bologna, Bologna, Italy

OPEN ACCESS

EDITED BY
Alfons O. Hamm,
University of Greifswald, Germany

REVIEWED BY
Meera Mary Sunny,
Indian Institute of Technology Gandhinagar, India
Diivta Singh,
Ahmedabad University, India

*CORRESPONDENCE
Maurizio Codispoti
✉ maurizio.codispoti@unibo.it

RECEIVED 16 October 2023
ACCEPTED 12 January 2024
PUBLISHED 07 February 2024

CITATION
Ferrari V, Canturi F, De Cesarei A and Codispoti M (2024) Sustained training with novel distractors attenuates the behavioral interference of emotional pictures but does not affect the electrocortical markers of emotional processing.
Front. Psychol. 15:1322792.
doi: 10.3389/fpsyg.2024.1322792

Introduction: Research has recently shown that behavioral interference prompted by emotional distractors is subject to habituation when the same exemplars are repeated, but promptly recovers in response to novel stimuli. The present study investigated whether prolonged experience with distractors that were all novel was effective in shaping the attentional filter, favoring stable and generalizable inhibition effects.

Methods: To test this, the impact of emotional distractors was measured before and after a sustained training phase with only novel distractor pictures, and that for a group of participants depicted only a variety of neutral contents, whereas a different group was exposed only to emotional contents.

Results: Results showed that emotional interference on reaction times was attenuated after the training phase (compared to the pre-test), but emotional distractors continued to interfere more than neutral ones in the post-test. The two groups did not differ in terms of training effect, suggesting that the distractor suppression mechanism developed during training was not sensitive to the affective category of natural scenes with which one had had experience. The affective modulation of neither the LPP or Alpha-ERD showed any effect of training.

Discussion: Altogether, these findings suggest that sustained experience with novel distractors may attenuate attention allocation toward task irrelevant emotional stimuli, but the evaluative processes and the engagement of motivational systems are always needed to support the monitoring of the environment for significant cues.

KEYWORDS

emotional scenes, training, behavioral interference, LPP, Alpha-ERD

1 Introduction

In our daily life, whether we are exploring the environment in search of something or someone, or navigating the web, it often happens that we run into important stimuli that involuntarily capture attention and interrupt ongoing goal-directed activities. Selective attention enables individuals to commit cognitive resources to significant elements in the visual environment while filtering irrelevant sensory input (Egeth and Yantis, 1997; Folk, 2015). It is well established that there are certain classes of stimuli that, when they are distractors, are more resistant to inhibition than others (Folk, 2015). Emotional stimuli are an example, especially those depicting sexual or blood/wound contents (Most et al., 2007; De Cesarei and Codispoti, 2008), which have a high attentional priority. Research has shown that emotional pictures engage attentional resources, and hence disrupt performance (i.e., elongate reaction time) in a variety of concurrent tasks (Hartikainen et al., 2000; Schimmack, 2005; Most et al., 2007; De Cesarei and Codispoti, 2008; Ferrari et al., 2017).

According to several studies, the viewing of emotional pictures activate corticolimbic motivational systems (appetitive and aversive) that, in turn, enhance attention allocation to efficiently process the stimulus itself (Öhman, 1992; Hamm et al., 2003; Bradley, 2009; Gottlieb, 2012; Codispoti et al., 2016; Mulckhuyse, 2018). In terms of electrocortical activity, it is well established that emotional pictures (pleasant and unpleasant) elicit a larger late positive potential (LPP) and Alpha event-related desynchronization (Alpha ERD) than neutral images (Schupp et al., 2006; De Cesarei and Codispoti, 2011; Ferrari et al., 2020; Schubring and Schupp, 2021; Ferrari et al., 2022), and these cortical modulatory effects have been interpreted as reflecting both the engagement of attentional resources by emotional stimuli and the activation of motivational systems (Schupp et al., 2006; Lang et al., 2008; Ferrari et al., 2011; Weinberg and Hajcak, 2011; for a review focusing on similarities and differences between these measures see Codispoti et al., 2023).

It has been suggested that being repeatedly exposed to irrelevant events leads to more efficient filtering of those events (Kelley and Yantis, 2009; Vecera et al., 2014). Mere stimulus repetition is also effective in attenuating attentional capture by emotional distractors (Codispoti et al., 2016; Ferrari et al., 2022). However, emotional interference recovered when novel stimuli were presented after the habituation phase, indicating that the filtering mechanism was finely tuned regarding the specific stimulus used throughout habituation and did not apply to similar emotional exemplars, such as those presented in the novel phase (Wendt et al., 2011; Codispoti et al., 2016).

Research seems to indicate that attentional capture by emotional distractors can be attenuated even with novel stimuli (i.e., never repeated) by increasing the overall distractor frequency (Micucci et al., 2020). When participants were rarely exposed to distractors (20% of total trials, 10% emotional, 10% neutral), emotional pictures captured more attentional resources compared with neutral images, causing a behavioral interference (RT slowdown) with the ongoing task. However, this RT emotional interference (emotional vs. neutral) decreased when the overall frequency of distractors increased (80% of total trials, 40% emotional, 40% neutral). The emotional interference was attenuated by distractor frequency even when rare emotional distractors appeared among frequent neutral distractors (80% of total trials, 10% emotional, 70% neutral). In the same study (Micucci et al., 2020), distractor frequency (using entirely novel stimuli), moreover, did not attenuate the affective modulation of the late positive potential, suggesting that the high occurrence of distractors does not proactively prevent the processing of emotional task-irrelevant cues. Distractor repetition (same exemplar) was, on the other hand, effective in reducing both behavioral interference as well as the LPP modulation (Ferrari et al., 2022) when distractors were task-irrelevant pictures presented in peripheral vision while a central discrimination task was being performed.

These series of studies support the hypothesis that attentional capture prompted by emotional stimuli is a flexible mechanism that can be temporarily affected by contextual factors (distractor frequency) and learning (habituation), with effects at different response levels (i.e., behavioral interference and LPP). Here, we aim to extend the assessment of experience-related factors that can be effective in attenuating the interference of emotional distractors, with a specific question regarding whether the experience with distractors that accumulates over time is effective in shaping the attentional filter, favoring stable and generalizable inhibition effects. In other words, can attentional capture by novel and emotional distractors be attenuated through prolonged experience over time? We already know that experience with the same distractors (same exemplars repeated multiple times) is only effective in attenuating the interference of those distractors, but it does not generalize toward new, subsequently presented, distractors. The literature, on the other hand, indicates that when the trained distractors are variable, the attentional filter encodes multiple features and encompasses broad representations, with the advantage of generalizing suppression more easily beyond the specific trained exemplars to other potential novel stimuli (Dixon et al., 2009; Kelley and Yantis, 2009, 2010; Vatterott and Vecera, 2012; Vatterott et al., 2018). Therefore, the present study introduced sustained experience with distractors that were all new (novel exemplars) in that they were never repeated throughout the study, and tested whether this experience affected the emotional interference of subsequently appearing distractors. Thus, similar to previous studies, emotional and neutral pictures consisted of task-irrelevant stimuli presented in peripheral vision while a central discrimination task was being performed. After an initial block of trials (pre-test) in which the enhanced interference of emotional distractors was measured in terms of behavioral and brain responses, the same task continued to be performed in a practice phase, which had the goal of providing a sustained and prolonged experience with distractors (twice as many trials as the pre-test). A final block (post-test) was then introduced to assess the amount of attentional capture by emotional pictures compared to the pre-test. Thus, the main question of the study was whether emotional interference may benefit from sustained experience with novel distractors. The second question concerns the specific content of distractors during the practice phase. Do observers need specific practice (experience) with emotional distractors in order to effectively inhibit their processing? Given the obligatory nature of emotional processing, we may expect that general experience with distractors is not sufficient to efficiently shield the attentional set from distraction. More sustained experience with wholly novel emotional distractors might help tune a specific filter based on the perceptual similarities within the semantic category (e.g., erotica), creating a situation that is more similar to that of repeated distractors (habituation paradigm, Ferrari et al., 2022) which is highly effective in preventing emotional interference. The goal of the present study was to investigate whether the filtering becomes effective with general experience with simply neutral (non-emotional) distractors, or whether specific emotional practice is needed to prompt a stable distractor inhibition mechanism. Thus, one group of subjects underwent a practice phase with solely neutral distractors, whereas a different group had experience with distractors that were all emotional (a between-subject design, where only the type of distractors used in the practice phase differed).

Distractor filtering may occur at various stages of processing. Therefore, besides behavioral interference, indexed by RTs, we also examined two cortical indexes of emotional processing, the LPP and Alpha-ERD, to better clarify at which stage the filter can operate. Sustained exposure to task-irrelevant distractors may affect the activation of motivational systems, preventing the cascade of perceptual and motor responses that are typically prompted by the detection of emotional stimuli. Alternatively, motivational systems might continue to be engaged after an extensive exposure to novel distractors to support some fundamental sensory processing, without necessarily interfering with the ongoing task performance. Although a reduction in emotional interference can be predicted by both these scenarios, emotional effects at the cortical level may reveal the extent to which frequent distractors are actually ignored.

Research has shown that Alpha-ERD emotional modulation is unaffected by top-down factors, such as task-related processes (Schubring and Schupp, 2019; Codispoti et al., 2023), or picture repetition (Ferrari et al., 2015; 2020; 2022; Schubring and Schupp, 2021). The affective modulation of the LPP is affected by stimulus repetition (Codispoti et al., 2007; Mastria et al., 2017), and there is evidence of stronger habituation when pictures are outside the attentional focus, and behave as distractors (Ferrari et al., 2022). Similarly, a prolonged experience with novel distractors may result in a narrowing of the attentional focus, with an effect also at the level of the LPP and Alpha ERD modulation.

While the topography of the overall LPP (regardless of picture content) does not vary depending on the hemifield of picture presentation, alpha activity has been repeatedly shown to decrease more in the hemisphere contralateral to the stimulus/target location (Bacigalupo Izquierdo and Luck, 2019; Murphy et al., 2020; Arana et al., 2022; Ferrari et al., 2022). Therefore, in the present study, we examined whether sustained experience with novel distractors resulted in reduced contralateral Alpha-ERD, possibly reflecting distractor filtering associated with an enhanced attentional focus on (central) target processing.

In previous studies, these cortical and behavioral (RTs: emotional vs. neutral interference) measures were used interchangeably (to some extent) to examine the effects of emotion on attention (MacNamara and Hajcak, 2009; Weinberg et al., 2021), and it has also been suggested that LPP and emotional interference are associated with each other during affective picture processing (Weinberg and Hajcak, 2011; Weinberg et al., 2021). A further aim of the present research is to explore the relationships among these neural and behavioral markers of emotional processing.

2 Method

2.1 Participants

A total of fifty-four (27 females; mean age = 25.2 years, SD = 4.6) healthy students participated as volunteers in the study, and all signed the informed consent before starting the experiment. Twenty-six students were randomly assigned to the "neutral training" protocol, and twenty-eight to the "emotional training" protocol. Because of technical problems, data from one participant in the neutral practice protocol were not included in the overall analysis. The study was approved by the Ethical Committee of the University of Parma. All participants had normal or corrected-to-normal visual acuity. We estimated sample size using GPower* (Faul et al., 2007), aiming to determine the number of participants necessary, in an ANOVA with one between-participant factors with two levels (neutral vs. emotional training group) and two within-participant factors (each one with two levels, Phase and emotional vs. neutral), to observe an effect size of at least $\eta^2_p = 0.07$ (medium effect size, Cohen, 1988), with 0.05 alpha-error probability, 80% power, and a correlation among repeated measures of 0.6. This analysis yielded 24 as the result.

2.2 Material

A total of 900 pictures of natural scenes were selected from the International Affective Picture System (IAPS; Lang et al., 2008), and from public domain pictures available on the Internet. Of these pictures, 30 depicted pleasant contents (erotica), 30 unpleasant contents (injured bodies) and 60 showed people in neutral contexts, and all of these were always presented in the pre-test or in the post-test (all pictures were counterbalanced across conditions). 480 stimuli depicted neutral contents from a wide variety of semantic categories, such as objects, animals, means of transportation, and outdoor or indoor scenes. Of these, 180 pictures were used as neutral fillers in the pre- and post-test for both groups (neutral and emotional groups). The remaining 300 were used for the neutral training group. For the emotional training group only, 300 pictures depicting emotional contents (erotica and injured bodies, equally distributed) were selected from public domain pictures available on the Internet to be presented during the practice phase.

Pictures of natural scenes served as distractor stimuli and were positioned to either the left or right of a central Gabor patch (sinusoidal gratings with a Gaussian envelope). The distance between the inner edge of the distractor image and the center of the Gabor patch was 4°.

The Gabor patch subtended a 5.3° × 5.3° visual angle and it could be horizontally or vertically oriented. Gabor patches were generated using custom MATLAB software by overlapping two distinct Gabor patches with the same frequencies but different orientation (0.94 and 9.4 cycles per degree of visual angle, respectively). Stimuli were displayed on a gray background.

Stimuli were presented on a 16-in monitor at 1024 × 768 resolution and at a refresh rate of 120 Hz. Stimulus presentation and data collection were performed using E-Prime software (Schneider et al., 2002).

2.3 Procedure

Upon arrival at the laboratory, participants signed an informed consent form. They were then seated in a recliner in a small, sound-attenuated, dimly lit room, and the EEG sensor net was attached. Participants sat in front of the computer monitor with their head supported by a chinrest. For all subjects the distance between their eyes and the monitor was 51 cm.

The experimental session consisted of three main phases: an initial Pre-Test, a Training Phase, and a final Post-Test. The Pre-Test and Post-Test phases were identical and consisted of 300 trials each in which distractors appeared randomly in 50% of the trials ($n = 150$). Of these distractors, 30 pictures depicted emotional (half pleasant and half unpleasant) contents, 30 neutral people, and the remaining 90 distractors were pulled from the neutral filler category. The training phase consisted of 600 trials, in which, again, distractors appeared in 50% of the trials and were exclusively neutral scenes for the neutral training group, and only emotional distractors for the emotional training group. Across participants of both groups, four stimulus sets with different pictures were equally rotated across conditions (pre-test and post-test) to make the results more generalizable in terms of stimulus exemplars.

Figure 1 shows the trial and the sequence of events of the experimental paradigm. In each trial, a Gabor patch appeared in the center of the screen for 150 msec. The participant's task was to determine, as quickly and accurately as possible, whether the Gabor patch was vertical or horizontal by pressing the corresponding keys with the index finger of the dominant hand. The intertrial interval was variable (1,000, 1,550, or 1,750 msec) and consisted of a gray screen. During this period, behavioral responses to the orientation task were collected. In distractor-present trials, a distractor picture was presented simultaneously with the Gabor patch, appearing equally often in the left or right visual field. Participants were explicitly informed that there would be a distractor in some trials and that it should be ignored. The task remained the same throughout the whole experiment. Before the beginning of the experiment, participants performed a short practice session (150 trials), in order to familiarize themselves with the task. Between each block a 5-min break was given. The experiment lasted for approximately 52 min.

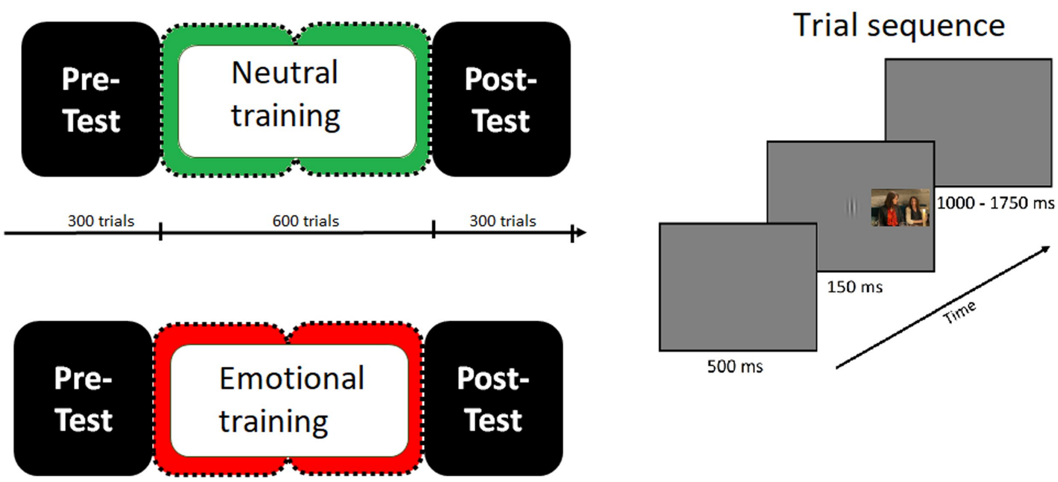


FIGURE 1
Schematic diagram showing the sequence of events in the present study. The trial sequence was the same over the whole experiment, with an initial dark-gray blank screen appearing for 500 msec, followed by a Gabor patch (target stimulus) presented for 150 msec. In half of the trials with a random occurrence, one picture of a natural scene appeared as a distractor stimulus simultaneously with the Gabor patch, flanking it to the left or right, and stayed on the screen until the Gabor patch disappeared. Participants were instructed to focus their attention on the Gabor patch and to determine its orientation (vertical or horizontal) by pressing one of two buttons while ignoring the distracting scenes. In the pre-test as well as in the post-test distractors were pictures depicting both emotional and neutral contents. In the practice phase, distractors were only neutral pictures for group 1 or only emotional pictures for group 2.

2.4 EEG recording and processing

Electroencephalogram (EEG) was recorded at a sampling rate of 1,000 Hz using a 59 channel Electro-Cap connected to a SA Instrument CO (San Diego, CA) UF-64/72BA amplifier and in-house developed software. Impedance of each sensor was kept below 10 kΩ. Eye movements were recorded at a sampling rate of 500 Hz from two bipolar couples of electrodes, one pair placed 1 cm above and below the right eye, and the other 1 cm from the external corner of both eyes. Both EEG and ocular signal were on-line filtered from 0.01 to 100 Hz. E-prime software synchronized the presentation of the stimuli and triggered EEG recording in each trial. Off-line analysis was performed using Emegs (Peyk et al., 2011). First, eye movements were subtracted from the EEG on a trial-by-trial basis, based on the data from the monopolar horizontal and vertical EOG, using a regressive procedure (Gratton et al., 1983). Data were low-pass filtered at 30 Hz. Trials and sensors containing artifacts were detected through a statistical procedure (Junghofer et al., 2000). In each trial, if a high number of neighboring bad sensors was present, then the whole trial was discarded; for the remaining trials, sensors containing artifacts were replaced by interpolating the nearest good sensors. The percentage of good trials was 85%, and this percentage did not significantly change across blocks or conditions. Finally, data were re-referenced to the average of all channels. The average of the 200 ms pre-stimulus baseline was subtracted to the obtained waveform. Processed data were averaged for each Phase (Pre-test and Post-test) and Trial type (distractor absent; emotional and neutral distractors). ROI and time interval of interest were identified both through visual inspection and according to previous studies (Micucci et al., 2020; Ferrari et al., 2022). The LPP was scored as the average of the ERP waveform in the 450 and 900 msec period after stimulus onset at the centro-parietal sensor group (see Figure 2 for the scalp topography of the LPP emotional modulation).

For time-frequency analysis, no low-pass filtering was applied on the EEG signal, but the correction of eye movements, as well as the artifact detection and sensor interpolation, was similar to the ERP analysis. Data were convolved using complex Morlet's wavelet, varying in time and frequency with a Gaussian shape. The time frequency analysis was performed on single trial data using FieldTrip software through EMEGS (Peyk et al., 2011). The Morlet wavelet had a Gaussian shape, where the f/SD(f) ratio was set to 7, and the number of wavelet cycles was set to 5 (Tallon-Baudry et al., 1997). The range of analysis was from 4 to 80 Hz and analysis was performed in time windows from 1,000-ms before picture onset to 1,500 ms after picture onset in steps of 10 ms. As frequency resolution is maximal for low frequencies and minimal for high frequencies (Roach and Mathalon, 2008), the step between successive frequencies varied linearly from 0.5 Hz for the lowest frequencies to 5 Hz for the highest frequencies. All data were baseline corrected by subtracting the average alpha power of the pre-stimulus baseline (− 300 to −100 ms) from each data point. The baseline was calculated slightly earlier than stimulus onset to avoid the burst of oscillatory activity that starts before the onset of the stimulation, due to the artifact of the filter algorithm (Herrmann et al., 2005). The resulting event-related change in total power values (relative to baseline) are in decibels (dB) (Delorme and Makeig, 2004). Analyses of Alpha-ERD (8–14 Hz) were performed on a bilateral occipito-temporal sensor group (see Figure 3) over the same temporal window of the LPP (450–900 ms).

2.5 Data analysis

RT and EEG analyses were performed only on accurate trials (overall accuracy 96,4%), that is, when the orientation of the central gabor was correctly detected. For each participant, phase, and trial type, RTs above or below 3 SDs from the mean were discarded as outliers. Considering trials exclusion due to EEG artifacts or behavioral errors/outliers, the EEG signal (both LPP and Alpha-ERD) was analyzed on average over 24 trials per condition.

The same statistical design was applied to all measures analyzed in this study, with two within-subject factors: Phase (2: Pre-test, Post-test) and Trial type (3: distractor absent, emotional, neutral); one between-subject factor represented by the two groups of participants who underwent a different training protocol, one with entirely neutral distractors, the other with all distractors containing emotional content (training type). For each ANOVA test, we reported the partial η^2 squared statistic (η^2_p) indicating the proportion of variance that is explained by experimental conditions over the total variance.

3 Results

3.1 Behavioral data

Figure 2 illustrates the behavioral interference as a function of distractor content. The ANOVA performed on the whole statistical design (Phase x trial Type x Group) revealed a main effect of trial type $F(2,50) = 62.545$, $p < 0.0001$, $\eta^2_p = 0.714$, showing an expected RT slowdown with the occurrence of all distractor pictures, compared to distractor absent trials $Fs(1,51) > 76$; $ps < 0.0001$, $\eta^2_p > 0.741$. Distractor interference was enhanced for emotional compared to neutral distractors, $F(1,51) = 30.605$, $p < 0.0001$, $\eta^2_p = 0.375$.

There was also an overall decrease of RT across the two phases $F(1,51) = 14.854$, $p < 0.001$, $\eta^2_p = 0.226$, and the interaction phase x trial type $F(2,50) = 8.482$, $p < 0.001$, $\eta^2_p = 0.253$ indicated that this decrement that followed the training phase significantly affected the RT emotional interference, which was smaller in the post-test compared to the pre-test (phase x emotional vs. neutral distractors, $F(1,51) = 13.161$; $p < 0.001$, $\eta^2_p = 0.205$). Although reduced, emotional interference was still highly significant in the post-test, $F(1,51) = 13.198$, $p < 0.001$, $\eta^2_p = 0.206$. The between-subject factor that refers to the different distractor category (all neutral or all emotional) used during the training phase did not show any significant effect, suggesting that the attenuation of emotional interference after the sustained training session was not specifically related to the type of experience with distractor content [2 × 3 × 2, $F(3,50) = 2.359$, $p > 0.05$, $\eta^2_p = 0.09$]. Moreover, a specific test on the affective modulation, that is, on the difference between emotional and neutral distractors, with the two factors, phase x group (training type), revealed no significant interaction effect, $F(1,51) < 0.1$, $p = 0.454$, $\eta^2_p = 0.011$.

The ANOVA on accuracy did not reveal any significant effects involving the three factors, or their interactions.

3.2 Late positive potential (LPP)

Figure 3 illustrates the LPP enhancement for emotional, compared to neutral, distractors, over the centro-parietal region. The ANOVA in the LPP window revealed a main effect of Trial Type, $F(2,50) = 37.928$, $p < 0.0001$, $\eta^2_p = 0.603$, and of Phase, $F(1,51) = 13.742$, $p < 0.001$, $\eta^2_p = 0.212$. Distractor occurrence [any distractor, $Fs(1,51) > 7.591$, $ps < 0.01$, $\eta^2_p > 0.130$] prompted a significant increase in the LPP magnitude, compared to distractor absent trials, and the largest positivity was found for emotional distractors, compared to neutral people, $F(1,51) = 54$, $p < 0.0001$, $\eta^2_p = 0.515$. Although over time (pre-test vs. post-test) the overall LPP amplitude was attenuated, this decrease did not differ as a function of distractor content [phase x trial type, $F(2,50) < 1$, $p = 0.283$, $\eta^2_p = 0.49$], indicating that the LPP affective modulation (difference between emotional and neutral distractors) was unaffected by the extended practice with novel distractors. Accordingly, the type of distractors used in the training did not prompt any difference in the LPP modulation between the pre- and the post-test either [phase x trial type x group, $F(2,50) = <1$, $p = 0.883$, $\eta^2_p = 0.005$]; in fact, the two groups of participants showed no significant difference in cortical modulation between the two phases, regardless of what kind of practice they had carried out with distractors.

3.3 Brain oscillations: Alpha-ERD

Figure 4 illustrates Alpha ERD as a function of distractor content and position (left and right hemifield). The power in the Alpha band was clearly reduced compared to the baseline when a peripheral distractor was present compared to absent, and this desynchronization was enhanced for emotional, compared to neutral, pictures in the pre-test, as well as in the post test.

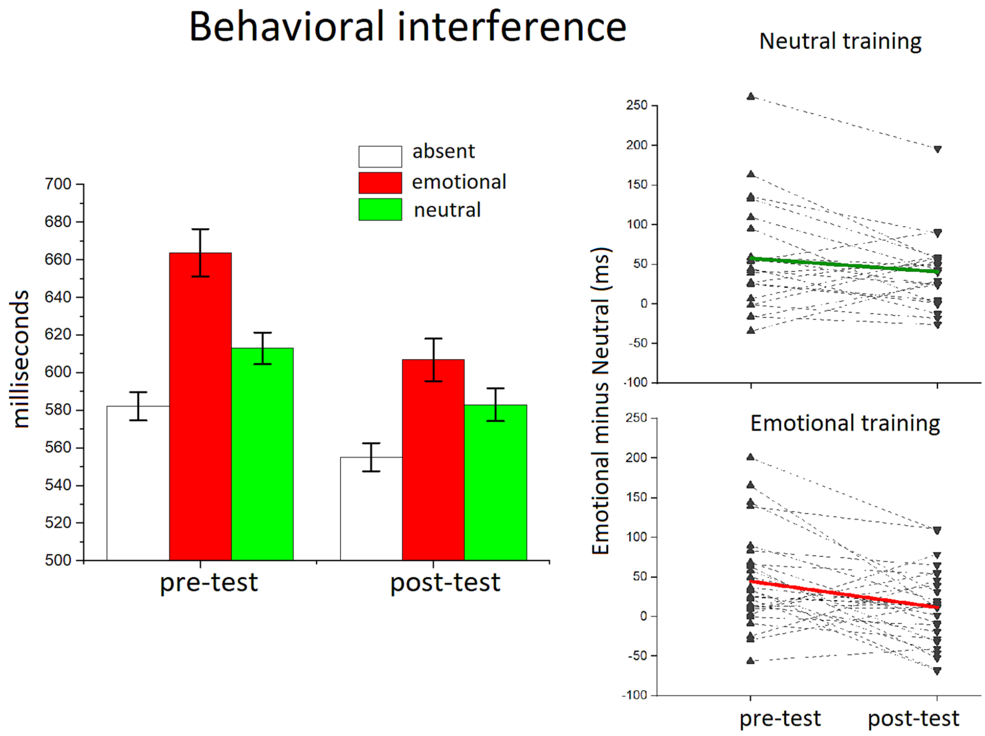


FIGURE 2
The effects of distractor occurrence on the LPP amplitude. **(A)** Grand-averaged ERP waveforms (average across the sensor cluster) for emotional and neutral distractors in the pre-test block. Insets show the scalp topography (450–900 msec) of the difference in the LPP between emotional and neutral distractors. **(B)** The bar graphs show the mean of the LPP amplitude (window 450–900 ms) for distractor-absent, emotional, and neutral distractors in the pre- and the post-test.

The ANOVA in the alpha band revealed a significant modulation as a function of trial type, $F(2,50) = 19.968$, $p < 0.0001$, $\eta^2_p = 0.444$, with the largest desynchronization for trials with the occurrence of emotional distractors, and the smallest for distractor absent trials. Alpha-ERD for neutral distractor trials was significantly larger compared to distractor absent trials, $F(1,52) = 17.297$, $p < 0.001$, $\eta^2_p = 0.253$, and significantly smaller compared to emotional trials, $F(1,52) = 17.727$, $p < 0.001$, $\eta^2_p = 0.254$. The overall Alpha-ERD was slightly attenuated in the post-test compared to the pre-test, $F(1,51) = 5.144$, $p < 0.05$, $\eta^2_p = 0.092$, but the magnitude of this effect did not differ across trial type conditions. The between-subject factor (training type) was not involved in any significant interaction.

An additional analysis focused on the contra/ipsi lateral Alpha-ERD to distractor-present vs. distractor-absent trials, in order to evaluate whether the alpha activity in response to lateralized distractors was affected by the training. The distractor contralateral alpha activity (distractor minus absent) did not vary between the pre-test and the post-test, $F(1,48) = 1.86$, $p = 0.179$, $\eta^2_p = 0.037$. Similarly, the distractor ipsilateral alpha activity (distractor minus absent) did not vary between the pre-test and the post-test, $F(1,48) = 2.28$, $p = 0.137$, $\eta^2_p = 0.045$.

3.4 Cortical (LPP and Alpha-ERD) and behavioral interference: between-subject correlations

In order to directly assess the relationship between different indices of emotional processing (behavioral interference, LPP, and Alpha-ERD), Pearson's correlation coefficients were calculated using the difference scores (emotional minus neutral), separately for the pre- and the post-test. None of the correlations were significant in the pre-test ($-0.18 > \text{rs} < 0.07$, $\text{ps} > 0.19$) or in the post-test ($-0.25 > \text{rs} < 0.19$, $\text{ps} > 0.06$).

4 Discussion

The goal of the present study was to investigate the effects of training on the emotional interference of novel distractors depicting natural scenes. The extended experience with distractors throughout several blocks of trials prompted an attenuation of emotional interference between the post-test and the pre-test. This effect was independent of the type of experience with distractor content, since it occurred to the same extent in both groups of participants, for those whose training involved neutral distractors as well as for those who were exposed to emotional pictures during training. Unlike the behavioral interference, the affective modulation of both cortical indexes of emotional processing, the late positive potential and the Alpha-ERD, was unaffected by the amount and type of distractor exposure.

Previous repetition studies reported emotional distractor suppression after several repetitions of the same exemplars (Ferrari et al., 2022); here, the emotional interference was reduced over trials despite distractors consisting of a variety of novel natural scenes that were never repeated across the experiment. These results are in line with what was found in a similar paradigm in which the exposure to

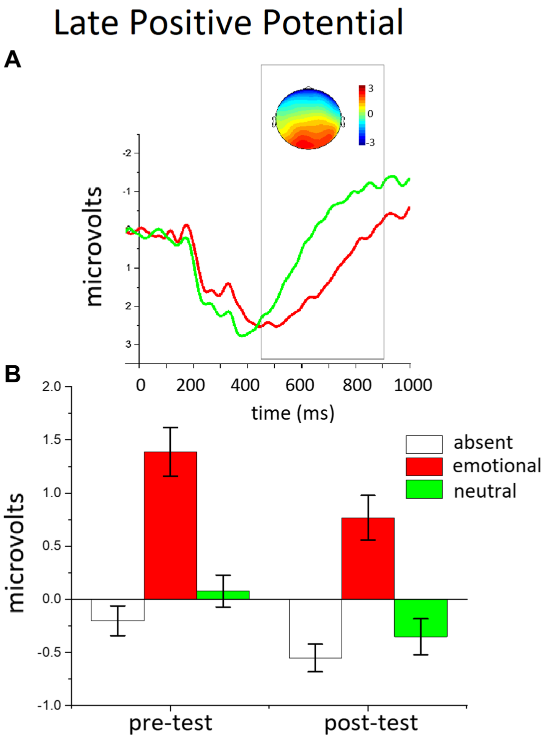


FIGURE 3
The effects of distractor occurrence on the Alpha-ERD. **(A)** Time-frequency plot of the emotional-neutral difference at occipitotemporal sensor sites, regardless of distractor laterality. **(B)** Topography of alpha power changes (450–900ms window) for emotional and neutral distractors appearing on the left or on the right of the visual hemifield. **(C)** The bar graphs show the mean of the alpha power changes (window 450–900ms) for distractor-absent, emotional and neutral distractors in the pre- and the post-test.

novel distractors varied as a function of distractor frequency occurrence (Micucci et al., 2020), suggesting that sustained experience with distractors can affect emotional capture even when distractors are novel stimuli (never repeated). A possible factor accounting for these effects could be the narrowing of spatial attention: Is the decline of emotional interference due to a specific inhibition of any sensory stimulus appearing in the distractor locations, preventing the identification of the affective category of the stimulus and the consequent engagement of motivational systems? In this respect, findings from cortical measures help to rule out this hypothesis. Indeed, the emotional nature of the distractors modulated both LPP and Alpha-ERD without showing any training effect, indicating that the reduction in the emotional interference effect cannot be explained in terms of a spatially specific inhibition of the distractor locations. Consistently, we did not find a reduction in the controlateral Alpha-ERD between the pre- and the post-test. These findings suggest that repetitive experience attenuates emotional interference, but it does not proactively prevent the processing of emotional distractors. A similar pattern of results was observed when the exposure to distractors was manipulated through distractor frequency occurrence (Micucci et al., 2020). Moreover, these findings are not consistent with a mere attention-capture interpretation of the affective modulation of the LPP and of Alpha-ERD, but provide further support that these cortical markers reflect the engagement of corticolimbic motivational systems in a mandatory fashion, even when further allocation of attention to emotional stimuli is attenuated.

It should be noted that while in previous studies emotional interference disappeared after a few distractor repetitions (Codispoti et al., 2016; Ferrari et al., 2022), here extensive experience with distractors determined a decrease in this effect which, however, continued to persist in the post-test, after over 900 trials. Moreover, it is well established that after substantial affective habituation, the occurrence of new stimuli in a final block (novel phase) was sufficient to reinstate an emotional effect (dishabituation) on several orienting measures (i.e., heart rate, skin conductance, pupil dilation, LPP; see also emotional interference). These findings, together with the somewhat weak effects of training with novel distractors observed in the present study, indicate that it is likely that the orienting mechanism is tuned on the specific exemplar that we directly experience, without generalization that spreads to the entire semantic category to which natural scenes belong, or to simple features that are shared between scenes, e.g., blood in unpleasant pictures (Gati and Ben-Shakhar, 1990). This interpretation is supported even more convincingly by the absence of an enhanced effect of the training involving emotional images, compared to the neutral training session, once again proving that the implicit learning to ignore emotional distractors, unlike other forms of implicit learning (e.g., Gordon and Holyoak, 1983), is built on the stimuli experienced, and does not generalize to similar exemplars.

It has also been suggested that behavioral interference by emotional stimuli may be solidly associated with the affective modulation of the LPP, both of these indexing attention allocation (Weinberg and Hajcak, 2011; Weinberg et al., 2021). The present study indicates that, although LPP, Alpha-ERD, and RTs are modulated by motivational significance (emotional arousal) during the viewing of novel pictures, they are differentially affected by sustained experience with novel distractors. Additionally, in the present study, there is no significant or close-to-significant correlation between behavioral interference and the LPP/Alpha ERD (neither regarding the absolute values nor for the emotional vs. neutral differentials). Moreover, a dissociation between the LPP and behavioral interference has been described in previous habituation studies, in which behavioral emotional interference waned after only a few presentations of the same distractor, whereas the LPP amplitude was still enhanced for emotional, compared with neutral, distractors despite picture repetition (Codispoti et al., 2006, 2016; Ferrari et al., 2022). These results do not support the hypothesis that the affective modulation of the LPP indexes attentional engagement with visual stimuli uniquely associated with the subsequent behavioral interference (RT slowdown) as previously proposed by Weinberg and colleagues (Weinberg et al., 2021).

Although the LPP and the Alpha-ERD share some similarities in terms of emotional modulation (De Cesarei and Codispoti, 2011; Ferrari et al., 2022), both being unaffected by training, they may reflect partially distinct processes engaged in emotional picture processing. Indeed, no correlation was found across participants between the emotional modulation of the LPP and the Alpha-ERD in the present study, or in previous studies (De Cesarei and Codispoti, 2011; Parvaz et al., 2015; see also Li et al., 2020, for dissociation in pain perception).

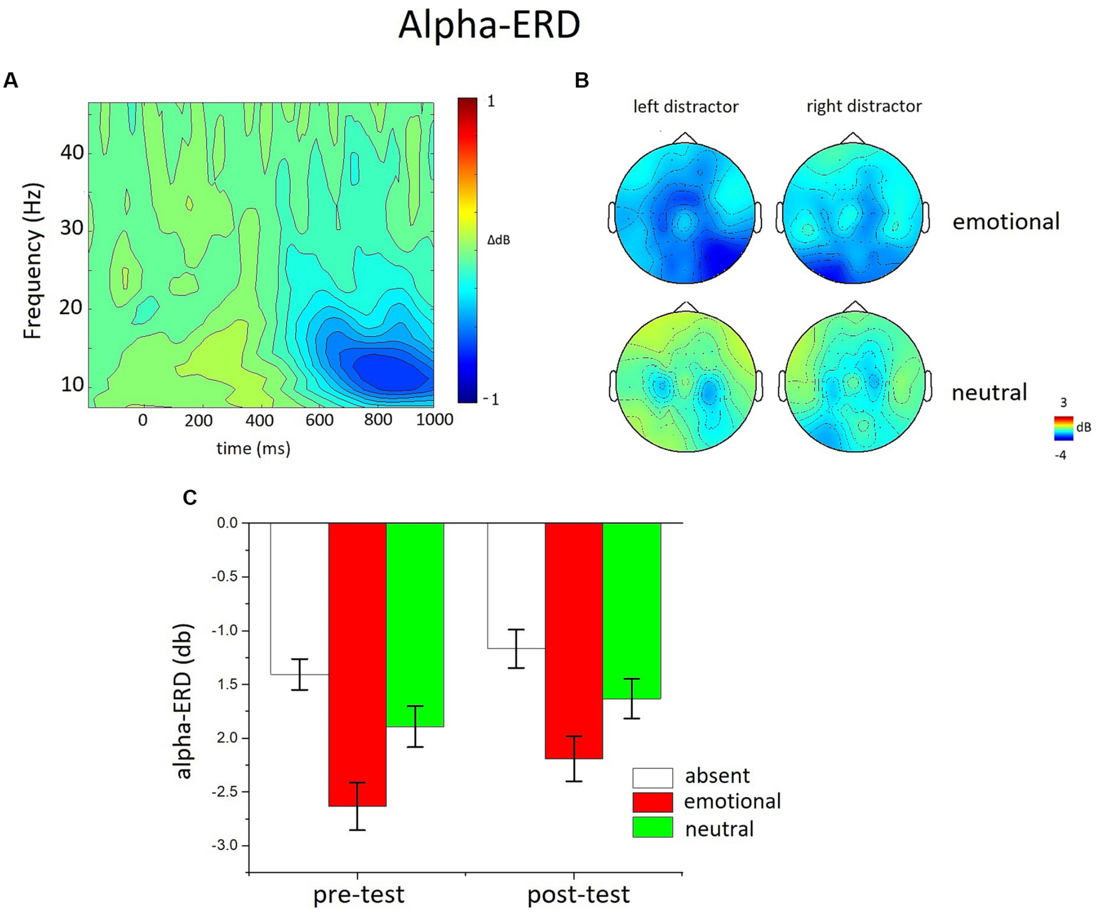


FIGURE 4
RTs in the discrimination orientation task for each trial type. Behavioral interference is plotted as a function of block, showing that the RT slowdown was maximum with the occurrence of emotional distractors, compared with neutral distractors or trials with no distractors. The emotional interference was clearly attenuated in the post-test. Error bars show ±1 SEM calculated within participants using the method of O'Brien et al. (2014). The inset shows the single subject plots of the emotional interference (emotional minus neutral) in the pre and post-test for each training group.

From the present study, it emerges that the visual perceptual system is extremely efficient in detecting and processing novel complex natural scenes, even when they are completely irrelevant to the ongoing task and outside the attentional focus defined by the target occurrence. This initial stage of processing is very sensitive to perceptual novelty and it implies an automatic categorization process based on the motivational relevance of the stimuli, revealing what the mandatory task of the perceptual system is, namely monitoring the environment for potential threats or rewards (Donchin et al., 1978). In fact, at this stage, top-down mechanisms, such as task-relevance or experience, do not seem to play any role, as shown by the absence of any training effect on the LPP and the Alpha-ERD modulation. On the other hand, the behavioral interference depends on a more flexible mechanism.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving humans were approved by Research Ethics Board – University of Parma. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study. The individual(s) provided their written informed consent for the publication of any identifiable images or data presented in this article.

Author contributions

VF: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. FC: Data curation, Investigation, Methodology, Visualization, Writing – original draft. AC: Conceptualization, Formal analysis, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing. MC: Conceptualization, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Arana, L., Melcón, M., Kessel, D., Hoyos, S., Albert, J., Carretié, L., et al. (2022). Suppression of alpha-band power underlies exogenous attention to emotional distractors. *Psychophysiology* 59:e14051. doi: 10.1111/psyp.14051

Bacigalupo Izquierdo, F., and Luck, S. J. (2019). Lateralized suppression of alpha-band EEG activity as a mechanism of target processing. *J. Neurosci.* 39, 900–917. doi: 10.1523/JNEUROSCI.0183-18.2018

Bradley, M. M. (2009). Natural selective attention: orienting and emotion. *Psychophysiology* 46, 1–11. doi: 10.1111/j.1469-8986.2008.00702.x

Codispoti, M., De Cesarei, A., Biondi, S., and Ferrari, V. (2016). The fate of unattended stimuli and emotional habituation: behavioral interference and cortical changes. *Cogn. Affect. Behav. Neurosci.* 16, 1063–1073. doi: 10.3758/s13415-016-0453-0

Codispoti, M., De Cesarei, A., and Ferrari, V. (2023). Alpha- band oscillations and emotion: a review of studies on picture perception. *Psychophysiology* 60:e14438. doi: 10.1111/psyp.14438

Codispoti, M., Ferrari, V., and Bradley, M. M. (2006). Repetitive picture processing: autonomic and cortical correlates. *Brain Res.* 1068, 213–220. doi: 10.1016/j.brainres.2005.11.009

Codispoti, M., Ferrari, V., and Bradley, M. M. (2007). Repetition and event-related potentials: distinguishing early and late processes in affective picture perception. *J. Cogn. Neurosci.* 19, 577–586. doi: 10.1162/jocn.2007.19.4.577

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (*2nd Edn*). Hillsdale, NJ: Lawrence Erlbaum Associates Publishers.

De Cesarei, A., and Codispoti, M. (2008). Fuzzy picture processing: effects of size reduction and blurring on emotional processing. *Emotion* 8, 352–363. doi: 10.1037/1528-3542.8.3.352

De Cesarei, A., and Codispoti, M. (2011). Affective modulation of the LPP and α-ERD during picture viewing. *Psychophysiology* 48, 1397–1404. doi: 10.1111/j.1469-8986.2011.01204.x

Delorme, A., and Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21. doi: 10.1016/j.jneumeth.2003.10.009

Dixon, M. L., Ruppel, J., Pratt, J., and De Rosa, E. (2009). Learning to ignore: acquisition of sustained attentional suppression. *Psychon. Bull. Rev.* 16, 418–423. doi: 10.3758/PBR.16.2.418

Donchin, E., Ritter, W., and McCallum, W. C. (1978). Cognitive psychophysiology: the endogenous components of the ERP. *Event Related Brain Potentials Man* 349:411. doi: 10.1016/B978-0-12-155150-6.50019-5

Egeth, H. E., and Yantis, S. (1997). Visual attention: control, representation, and time course. *Annu. Rev. Psychol.* 48, 269–297. doi: 10.1146/annurev.psych.48.1.269

Faul, F., Erdfelder, E., Lang, A. G., and Buchner, A. G. (2007). Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods.* 39, 175–91. doi: 10.3758/bf03193146

Ferrari, V., Bradley, M. M., Codispoti, M., and Lang, P. J. (2011). Repetitive exposure: brain and reflex measures of emotion and attention. *Psychophysiology* 48, 515–522. doi: 10.1111/j.1469-8986.2010.01083.x

Ferrari, V., Bradley, M. M., Codispoti, M., and Lang, P. J. (2015). Massed and distributed repetition of natural scenes: Brain potentials and oscillatory activity. *Psychophysiology.* 52, 865–872. doi: 10.1111/psyp.12424

Ferrari, V., Bruno, N., Chattat, R., and Codispoti, M. (2017). Evaluative ratings and attention across the life span: emotional arousal and gender. *Cognit. Emot.* 31, 552–563. doi: 10.1080/02699931.2016.1140020

Ferrari, V., Canturi, F., and Codispoti, M. (2022). Stimulus novelty and emotionality interact in the processing of visual distractors. *Biol. Psychol.* 167:108238. doi: 10.1016/j.biopsycho.2021.108238

Ferrari, V., Codispoti, M., Cardinale, R., and Bradley, M. M. (2008). Directed and motivated attention during processing of natural scenes. *J. Cogn. Neurosci.* 20, 1753–1761. doi: 10.1162/jocn.2008.20121

Ferrari, V., Mastria, S., and Codispoti, M. (2020). The interplay between attention and long-term memory in affective habituation. *Psychophysiology* 57:e13572. doi: 10.1111/psyp.13572

Folk, C. L. (2015). "Controlling spatial attention: lessons from the lab and implications for everyday life" in *The handbook of attention*. eds. J. M. Fawcett, E. F. Risko and A. Kingstone (Cambridge, MA: MIT Press), 3–25.

Gati, I., and Ben-Shakhar, G. (1990). Novelty and significance in orientation and habituation: a feature-matching approach. *J. Exp. Psychol. Gen.* 119, 251–263. doi: 10.1037/0096-3445.119.3.251

Gordon, P. C., and Holyoak, K. J. (1983). Implicit learning and generalization of the" mere exposure" effect. *J. Pers. Soc. Psychol.* 45:492. doi: 10.1037/0022-3514.45.3.492

Gottlieb, J. (2012). Attention, learning, and the value of information. *Neuron* 76, 281–295. doi: 10.1016/j.neuron.2012.09.034

Gratton, G., Coles, M. G., and Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484. doi: 10.1016/0013-4694(83)90135-9

Hamm, A. O., Schupp, H. T., and Weike, A. I. (2003). *Motivational Organization of Emotions: Autonomic changes, cortical responses, and reflex modulation*. Oxford: Oxford University Press.

Hartikainen, K. M., Ogawa, K. H., and Knight, R. T. (2000). Transient interference of right hemispheric function due to automatic emotional processing. *Neuropsychologia* 38, 1576–1580. doi: 10.1016/S0028-3932(00)00072-5

Herrmann, C. S., Grigutsch, M., and Busch, N. A. (2005). "11 EEG oscillations and wavelet analysis" in *Event-related potentials: A methods handbook*. ed. T. C. Handy (Cambridge, MA: MIT Press), 229.

Junghofer, M., Elbert, T., Tucker, D. M., and Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology* 37, 523–532. doi: 10.1111/1469-8986.3740523

Kelley, T. A., and Yantis, S. (2009). Learning to attend: effects of practice on information selection. *J. Vis.* 9, 1–18. doi: 10.1167/9.7.16

Kelley, T. A., and Yantis, S. (2010). Neural correlates of learning to attend. *Front. Hum. Neurosci.* 4:216. doi: 10.3389/fnhum.2010.00216

Lang, P. J., Bradley, M. M., and Cuthbert, B. N. (2008). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8.*. Gainesville: University of Florida.

Li, Q., Joo, S. J., Yeatman, J. D., and Reinecke, K. (2020). Controlling for participants' viewing distance in large-scale, psychophysical online experiments using a virtual chinrest. *Sci. Rep.* 10:904. doi: 10.1038/s41598-019-57204-1

MacNamara, A., and Hajcak, G. (2009). Anxiety and spatial attention moderate the electrocortical response to aversive pictures. *Neuropsychologia* 47, 2975–2980. doi: 10.1016/j.neuropsychologia.2009.06.026

Mastria, S., Ferrari, V., and Codispoti, M. (2017). Emotional picture perception: repetition effects in free-viewing and during an explicit categorization task. *Front. Psychol.* 8:1001. doi: 10.3389/fpsyg.2017.01001

Micucci, A., Ferrari, V., De Cesarei, A., and Codispoti, M. (2020). Contextual modulation of emotional distraction: attentional capture and motivational significance. *J. Cogn. Neurosci.* 32, 621–633. doi: 10.1162/jocn_a_01505

Most, S. B., Smith, S. D., Cooter, A. B., Levy, B. N., and Zald, D. H. (2007). The naked truth: positive, arousing distractors impair rapid target perception. *Cognit. Emot.* 21, 964–981. doi: 10.1080/02699930600959340

Mulckhuyse, M. (2018). The influence of emotional stimuli on the oculomotor system: a review of the literature. *Cogn. Affect. Behav. Neurosci.* 18, 411–425. doi: 10.3758/s13415-018-0590-8

Murphy, J., Devue, C., Corballis, P. M., and Grimshaw, G. M. (2020). Proactive control of emotional distraction: evidence from EEG alpha suppression. *Front. Hum. Neurosci.* 14:318. doi: 10.3389/fnhum.2020.00318

O'Brien, B. C., Harris, I. B., Beckman, T. J., Reed, D. A., and Cook, D. A. (2014). Standards for reporting qualitative research: a synthesis of recommendations. *Acad Med.* 89, 1245–51. doi: 10.1097/ACM.0000000000000388

Öhman, A. (1992). "Orientingand attention: preferred preattentive processing of potentially phobic stimuli" in *Attention and information processing in infants and adults*. eds. B. A. Campbell, H. Hayne and R. Richardson (Hillsdale: Erlbaum), 263–295.

Parvaz, M. A., Moeller, S. J., Goldstein, R. Z., and Proudfit, G. H. (2015). Electrocortical evidence of increased post-reappraisal neural reactivity and its link to depressive symptoms. *Soc. Cogn. Affect. Neurosci.* 10, 78–84. doi: 10.1093/scan/nsu027

Peyk, P., De Cesarei, A., and Junghöfer, M. (2011). ElectroMagnetoEncephaloGraphy software (EMEGS): overview and integration with other EEG/MEG toolboxes. *Comput. Intell. Neurosci.* 2011:861705. doi: 10.1155/2011/861705

Roach, B. J., and Mathalon, D. H. (2008). Event-related EEG time-frequency analysis: an overview of measures and an analysis of early gamma band phase locking in schizophrenia. *Schizophr. Bull.* 34, 907–926. doi: 10.1093/schbul/sbn093

Schimmack, U. (2005). Attentional interference effects of emotional pictures: threat, negativity, or arousal? *Emotion* 5, 55–66. doi: 10.1037/1528-3542.5.1.55

Schneider, W., Eschman, A., and Zuccolotto, A. (2002). *E-prime reference guide*. Pittsburg, PA: Psychology Software Tools

Schubring, D., and Schupp, H. T. (2019). Affective picture processing: Alpha- and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology*, e13386. doi: 10.1111/psyp.13386

Schubring, D., and Schupp, H. T. (2021). Emotion and brain oscillations: high arousal is associated with decreases in alpha- and lower beta-band power. *Cereb. Cortex* 31, 1597–1608. doi: 10.1093/cercor/bhaa312

Schupp, H. T., Flaisch, T., Stockburger, J., and Junghöfer, M. (2006). Emotion and attention: event-related brain potential studies. *Prog. Brain Res.* 156, 31–51. doi: 10.1016/S0079-6123(06)56002-9

Tallon-Baudry, C., Bertrand, O., Delpuech, C., and Pernier, J. (1997). Oscillatory gamma-band (30–70 Hz) activity induced by a visual search task in humans. *J. Neurosci.* 17, 722–734. doi: 10.1523/JNEUROSCI.17-02-00722.1997

Vatterott, D. B., Mozer, M. C., and Vecera, S. P. (2018). Rejecting salient distractors: generalization from experience. *Atten. Percept. Psychophys.* 80, 485–499. doi: 10.3758/s13414-017-1465-8

Vatterott, D. B., and Vecera, S. P. (2012). Experience-dependent attentional tuning of distractor rejection. *Psychon. Bull. Rev.* 19, 871–878. doi: 10.3758/s13423-012-0280-4

Vecera, S. P., Cosman, J. D., Vatterott, D. B., and Roper, Z. J. (2014). "The control of visual attention: toward a unified account" in *Psychology of learning and motivation*, vol. *60* (Cambridge, MA: Academic Press), 303–347.

Weinberg, A., Correa, K. A., Stevens, E. S., and Shankman, S. A. (2021). The emotion-elicited late positive potential is stable across five testing sessions. *Psychophysiology* 58:e13904. doi: 10.1111/psyp.13904

Weinberg, A., and Hajcak, G. (2011). The late positive potential predicts subsequent interference with target processing. *J. Cogn. Neurosci.* 23, 2994–3007. doi: 10.1162/jocn.2011.21630

Wendt, J., Weike, A. I., Lotze, M., and Hamm, A. O. (2011). The functional connectivity between amygdala and extrastriate visual cortex activity during emotional picture processing depends on stimulus novelty. *Biol. Psychol.* 86, 203–209. doi: 10.1016/j.biopsycho.2010.11.009

frontiers | Frontiers in Psychology

TYPE Original Research
PUBLISHED 01 March 2024
DOI 10.3389/fpsyg.2024.1183996

OPEN ACCESS

EDITED BY
Alfons O. Hamm,
University of Greifswald, Germany

REVIEWED BY
Emma Claire Palmer-Cooper,
University of Southampton, United Kingdom
Hessel Engelbregt,
Ludwig Maximilian University of Munich,
Germany

*CORRESPONDENCE
Daniela M. Romano
✉ D.Romano@ucl.ac.uk

RECEIVED 10 March 2023
ACCEPTED 07 February 2024
PUBLISHED 01 March 2024

CITATION
Leung WL and Romano DM (2024) Autonomous sensory Meridian response as a physically felt signature of positive and negative emotions.
Front. Psychol. 15:1183996.
doi: 10.3389/fpsyg.2024.1183996

Autonomous sensory Meridian response as a physically felt signature of positive and negative emotions

Wai Lam Leung[1,2] and Daniela M. Romano[3,4]*

[1]Department of Psychology and Language Sciences, University College London, London, United Kingdom, [2]Department of Psychology, Institute of Psychiatry, Psychology and Neuroscience, King's College, London, United Kingdom, [3]Department of Information Studies, University College London, London, United Kingdom, [4]Institute of Artificial Intelligence, De Montfort University, Leicester, United Kingdom

Introduction: Current research on Autonomous Sensory Meridian Response (ASMR) assumes that ASMR is always accompanied by contentment, and it is distinct from frisson due to positive emotions. Thus, research investigations tend to limit their scope to solely focusing on the sensation of relaxation that ASMR induces. This study explores whether it is possible to have a different emotional experience and still perceive ASMR, testing the theory of ASMR as an amplifier of pre-existing emotion instead of a determination of positive affect.

Methods: The emotional arousal and valence, and mood changes of 180 ASMR-capable and incapable individuals were analysed using questionnaires after altering the affective interpretation associated with auditory ASMR (tapping) with visual priming to examine whether the primed emotion (fearful, relaxing, or neutral) could be amplified.

Results: It was found that an ASMR response occurred in all priming conditions, including the fear priming group. No significant difference was found in the emotional outcome or mood of the neutral and relaxing priming groups. Upon comparison with ASMR-incapable individuals, both the relaxing and neutral priming groups demonstrated the same affect, but greater potent for ASMR-capable. Individuals who appraised ASMR after visual fear priming demonstrated a significant decrease in positive emotional valence and increased arousal.

Conclusion: The findings suggest that ASMR occurs in both positive and negative emotional situations, suppressing contentment induction if ASMR stimuli are interpreted negatively and amplifying contentment when interpreted positively. While more research is needed, the results highlight that ASMR and frisson might describe the same phenomenon, both a physically felt signature of emotion. Therapeutic usage of ASMR should carefully select appropriate stimuli that emphasise contentment to avoid potential health risks associated with negative emotions until a further understanding of ASMR's affective parameters has been established.

KEYWORDS

autonomous sensory meridian response (ASMR), frisson, relaxation, fear, emotional valence, emotional arousal, neutral response, mood

1 Introduction

Autonomous Sensory Meridian Response (ASMR) is a perceptual response that begins from the scalp or spine and spreads across the body upon exposure to specific external triggers. Similar to frisson, a bodily sensation that involves a pleasurable chill that originates similarly around the head, neck, and spine area (Colver and El-Alayli, 2016), ASMR has been described as a form of "low-grade euphoria" due to its accompaniment with feelings of relaxation (Barratt and Davis, 2015; Fredborg et al., 2017; Poerio et al., 2018). Most research suggests that ASMR triggers vary from person to person, where triggers can be auditory, visual, tactile, or an amalgamation of them all (Barratt et al., 2017; Fredborg et al., 2017). ASMR stimuli are highly accessible through the internet; its accessibility being a key factor in its popularity over recent years.

The definition of ASMR has become ambiguous or overly subjective, promoting difficulties in distinguishing the differences between ASMR and other similar sensations, i.e., frisson or synaesthesia (Poerio et al., 2022). Where for example, synaesthesia, the involuntary perception that crosses over between senses (e.g., one is able to hear sounds and see colors), is common among those perceiving ASMR (Poerio et al., 2022). Descriptions of the ASMR sensation often mirror ones used to describe frisson (Panksepp, 1995; Blood and Zatorre, 2001). The similarity between the descriptions of the two phenomena has raised multiple stances within the research community. Some have argued that ASMR is a gentler subclass of frisson (Fairyington, 2014), whereas others would claim ASMR is unique to frisson and an independent sensation (Fredborg et al., 2017). Although the two are nearly indistinguishable at a descriptive level, empirical evidence has suggested that the differences between them predominantly lay upon the triggers that initiate them. For instance, frisson is mostly reported during music-listening and esthetic experiences compared to ASMR, which is more commonly experienced during mundane activities (e.g., physical examinations; Ahuja and Ahuja, 2019).

Due to the difficulties of distinguishing ASMR definition from frisson aside from ASMR-inducing contentment, research may have neglected contradicting claims related to non-relaxing ASMR experiences to maintain a forced distinction between the two. Although some empirical evidence does suggest that ASMR is associated with relaxation from psychometrics and physiological measurements, investigations tend to limit their scope to solely focus on the sensation of relaxation to avoid variating from the original non-scientific description of ASMR raised from the internet (see Barratt and Davis, 2015; Fredborg et al., 2017).

However, Kovacevich and Huron (2019) conducted a content analysis of the 30 most popular ASMR videos to examine the required features of ASMR. ASMR videos used less music, were quieter, and tended to use private settings as opposed to public settings when compared to control videos that were not ASMR-like in nature. This distinguishes ASMR from frisson, which is often reported to be under situations involving the presence of music and can occur during a loud listening session (Fredborg et al., 2017). However, both ASMR and control video ratings yielded a low Kappa statistic of 0.47, implying only moderate agreement within interrater reliability. Nevertheless, these findings were triangulated with self-report data, which found that using similar triggers induced ASMR in participants across different research studies (Barratt et al., 2017). This, therefore, shows the importance of distinguishing ASMR-like experiences from experiences of frisson. However, there are some similarities between ASMR and frisson, particularly in their physiological symptoms. For instance, pleasurable pilomotor activation (e.g., goosebumps) is shared across both sensations (Blood and Zatorre, 2001), and both would induce an increase in galvanic skin response (Guhn et al., 2007; Poerio et al., 2018). Thus, it is difficult to distinguish whether the bodily sensation is a result of ASMR if the context of triggers is insufficient or ambiguous. This ambiguity in identifying ASMR is even more problematic when research has shown that the triggers vary from person to person (Fredborg et al., 2017). Therefore, it is inherently difficult to distinguish the physiological sensations between ASMR and frisson.

Many have argued that the most critical component of distinguishing ASMR from other bodily sensations is the emotional outcome (Barratt and Davis, 2015; Del Campo and Kehle, 2016; Fredborg et al., 2017). As previously mentioned, ASMR is frequently associated with contentment and improvement in subjective wellbeing (Bishop et al., 2004; Barratt and Davis, 2015). For instance, Lohaus et al. (2023) demonstrated that ASMR sensations triggered simply by viewing ASMR videos are related to higher state relaxation and positive affect scores. This nature of the phenomenon became the primary reason why ASMR gained popularity because of its positive influence on emotion without complicated procedures. This led to comparisons between ASMR and mindfulness, a meditation method that involves distributing attention toward moment-by-moment experiences to repel negative emotions (Bishop et al., 2004). The premise of mindfulness is to gain awareness of the present and reduce reactiveness toward surrounding events or thoughts that may negatively influence our feelings (Lutz et al., 2008). The similarities between mindfulness and ASMR are not limited to the outcome but also procedural elements since recent research has discovered intertwined processes such as attentional control and openness to sensations (Fredborg et al., 2018). Thus, ASMR has caught some attention in the clinical field due to its potential to be an innovative medium for stress management and overall mental wellbeing (e.g., Cash et al., 2018).

However, esthetic chills such as frisson are often associated with excitement and physiological arousal (Grewe et al., 2009; Del Campo and Kehle, 2016). Supported by physiological measurements, the cardiac reaction upon experiencing the two sensations demonstrated a polarizing effect. While esthetic chills increase respiration rate and respiratory depth (Benedek and Kaernbach, 2011), ASMR reduces heart rate (Poerio et al., 2018), which can indicate relaxation (Pittig et al., 2013) since excitement and arousal are often associated with an increase in heart rate (Wulfert et al., 2005). However, Poerio et al. (2018) asked participants about their experiences with ASMR, and they reported increased levels of subjective excitement despite the reduction in heart rate. Regardless, the experience overall is still associated with contentment, which is not a component of frisson. Although distinguishing one phenomenon from another is undoubtedly an informative milestone in ASMR research, findings aligned with people's expectations have generated unnecessary strictness in bodily sensation classification. This strictness has manifested within internet communities—deeming reported anomalies within ASMR experience as preposterous. Claims regarding individuals experiencing non-relaxing ASMR are often disregarded due to the strict definition that ASMR must be accompanied by contentment. The findings of ASMR research can be misinterpreted by the layperson as findings not only alter the public's beliefs of ASMR but also the productivity of scientific research. ASMR research relies on content produced by the public, which may be reduced if people deliberately cancel meaningful debates on the topic. Astonishingly, these contradicting claims have remained resilient and begun to surface.

Non-relaxing ASMR has been reported on the internet for an extensive duration but was never acknowledged by the scientific community. For instance, a researcher of this project found that there are a few Reddit forum posts regarding ASMR as accompanied by fear responses. However, these experiences have caught little attention because they differ so strongly from our current understanding of the ASMR paradigm, and therefore, alternative experiences of ASMR have been neglected by public interest. One of these discussions depicted a panic episode when walking alone in the woods at night that was accompanied by ASMR (see I Started to Notice, 2016). Moreover, some YouTube videos have been suggested to be ASMR inducing even though they have unusual triggers; for example, videos of individuals walking into various locations (e.g., Aokigahara "Suicide" Forest & Cemetery; Rambalac, 2018). Although these videos may typically be associated with fear, they were suggested to be ASMR-inducing by both the uploader and the viewers, albeit with some uncertainty due to the divergence from the typical ASMR paradigm.

Another type of non-relaxing ASMR that has been reported is the association of ASMR with feelings of disgust. This experience is far more common than fear-related ASMR and is the reason why many individuals do not enjoy listening to ASMR-related stimuli. Most would argue that the reason for expressing disgust toward ASMR is related to misophonia, which refers to the hatred of sounds (Kovacevich and Huron, 2018). The typical trigger for misophonia is human-generated noises such as eating and breathing (Diamond-Flower, 2018; Rouw and Erfanian, 2018). Upon exposure to ASMR, an individual with misophonia would feel intense disgust, anger, or anxiety as an aversive response to avoid further exposure to the sound source (Wu et al., 2014). This experience of disgust is most prevalent in ASMR eating videos, where viewers either find it incredibly relaxing or disgusting (see Diamond-Flower, 2018; ima-lick-u, 2018).

Smith and Snider (2019) provided multiple references to ASMR artist's emphasis that ASMR media is intended for relaxation, stress, and anxiety management (Andersen, 2015), and there is undoubtedly a strong influence within the ASMR community to enforce the association between relaxation and ASMR. While most ASMR artists have enforced that the tingling sensation is a "relaxation response" (Andersen, 2015), no empirical findings can be confident that the response itself is relaxing by default. Specifically, based on the literature, we cannot distinguish whether ASMR is an esthetic chill-like experience with a relaxing nature or it is just a frisson generated by perceptual triggers that occur independently from emotions and acts as a physically felt signature of emotion, where contentment is just a by-product of interpretation since Smejka and Wiggs (2022) suggested that ASMR videos induce relaxation regardless of whether one can experience ASMR. However, the potency of relaxation has been shown to be more pronounced in individuals who can experience ASMR, which may indicate that ASMR sensations serve to amplify pre-existing emotions induced by the affective interpretation of the positive ASMR stimuli.

Thus, the assumption of ASMR sensation is not to determine emotion, but rather, to amplify pre-existing emotions. Perhaps one could attempt to manipulate one's affective positive interpretation of ASMR stimuli and cause ASMR sensation to amplify alternative emotions. Moreover, if such a hypothesis is correct, then there is a need to avoid narrowing our scope in believing that ASMR is always accompanied by relaxation and that there might be a need for re-evaluation in previous literature since most influential research has acquired samples from ASMR-related communities, which can be biased toward interpreting ASMR stimuli as relaxing. Anticipating ASMR as a relaxation response that produces biased positive affect findings is a self-fulfilling prophecy. More importantly, as mentioned earlier regarding the abundance of attention on ASMR being a potential therapeutic tool in the professional scene, if ASMR is indeed a signature or an overwhelming pre-existing emotion, then a stricter framework should be proposed when using ASMR in a therapeutic capacity, as it may be harmful when interpreted negatively. Thus, we intend to test whether it is possible to produce alternative emotional outcomes from ASMR by manipulating one's affective interpretation of the stimuli.

To test whether ASMR is a physically felt signature of an overwhelming emotion, researchers can prime the interpretation of the context of ASMR triggers to instigate a specific emotion with visual information (i.e., a video) beforehand. The visual information alone should induce an emotion that ASMR will later physically amplify (e.g., finger-tapping noises may be interpreted as blood dripping if primed by gory visuals beforehand, which may induce and amplify fear upon ASMR exposure). The priming material should be congruent to the ASMR trigger, meaning visual information must relate to the auditory ASMR trigger. Otherwise, the discrepancy between visual and auditory information may render priming ineffective.

The current experiment focuses on priming auditory ASMR triggers, specifically finger tapping, to test whether a negative emotion (e.g., fear) can be induced and physically amplified during the ASMR experience. Finger-tapping triggers were chosen due to their popularity and implementation in literature (Barratt et al., 2017; Fredborg et al., 2017). Most importantly, finger tapping is suitable for priming since it is more contextually neutral than triggers such as whispering, which is commonly misinterpreted sexually (Smith and Snider, 2019), or chewing, which may be considered ill-mannered and invoke disgust, for better control of manipulation across conditions. Furthermore, we chose to investigate fear due to its direct polarizing characteristics to contentment for better contrast in findings (McGinn and Kelly, 2018; Gu et al., 2019).

Overall, in this experiment, there will be three priming conditions: relaxation, fear, and neutral emotion (control condition) to evaluate the physical emotion amplification theory. Relaxation conditions will be primed using the conventional ASMR visuals, fear conditions using fear-related visuals, and control using emotionally neutral visuals. Concerning the control group, we hypothesize that the effect of ASMR on emotional amplification may be less potent than individuals primed with contentment-related visuals since previous studies have demonstrated that misophonia is influenced by the amount of contextual information given (see Edelstein et al., 2020). Thus, we hypothesized that control groups would demonstrate contentment induction due to the content impression of ASMR stimuli caused by media, as mentioned earlier, but not as strongly as the relaxation priming condition. Furthermore, individuals who do not normally have ASMR response toward the intended stimuli (i.e., ASMR-incapable group) will be tested for the three conditions as well to provide additional data for comparison with their capable counterparts to further affirm our theory. Thus, we hypothesize that ASMR-incapable individuals of each priming group will exhibit emotional valence and arousal of the same direction in relation to their ASMR-capable counterpart with lessened intensity as the absence of ASMR sensation in the ASMR-incapable group would disable amplification of the primed emotion.

2 Materials and methods

2.1 Participants

A total of 181 participants were recruited from the ASMR Reddit subforums[1] and through word-of-mouth. Reddit is a forum bringing together an English-speaking community with rules and terms and conditions written in English. Thus, participants' English comprehension abilities were assumed to be adequate for the experiment. Participants were entered in a prize draw to win a £10 Amazon voucher for their participation. One participant was excluded due to inappropriate responses during participation, which left 180 valid participants (104 male, 68 female, and 8 others). The ages of the participants ranged from 18 to 55 years ($M = 26.47$, $SD = 6.82$). The participant's origins can be divided into three main groups: 53 were European (29.4%), 79 were Americans (43.9%), and 48 were from other countries (26.7%; e.g., South East Asians, Eastern Asians, Africans, and South Americans). An a priori power analysis was conducted using G*Power version 3.1.9.7 (Faul et al., 2007) to determine the minimum samples size required for 2×3 factorial MANOVA at medium effect size ($f^2 = 0.15$; Cohen, 1988) and an alpha of 0.05 was 60 samples to achieve a power of 0.80.

Upon participation in the study, participants were labeled according to their ASMR ability (ASMR-capable or incapable) and the type of ASMR stimuli they were triggered by, which were assessed through the initial ASMR checklist (see Figure 1). Individuals who had not experienced ASMR and participants who were not triggered by auditory "tapping" stimuli were placed in the group labeled "ASMR Incapable" for the purpose of the experiment. Participants triggered by tapping were allocated to the "ASMR Capable" group (see Figure 1). The second criterion is crucial given that Fredborg et al. (2017) suggested that trigger type might vary among ASMR-capable individuals; this allows us to identify which participants can be triggered by the experimental stimuli and use ASMR-incapable individuals as a baseline to examine the effect of ASMR.

After assessing ASMR capability, participants are randomly allocated to either control, fear, or relaxation priming conditions (see Figure 1). Informed consent was obtained from all participants who took part in the study. All data were anonymized, and participants could withdraw at any point in the study. Ethical approval for this research was granted by the Department of Information Study Ethics Chair, University College London.

2.2 Measures

2.2.1 Experiment program

The study was created using an online experiment builder program Gorilla™. The experimental program can be accessed with a desktop, laptop, computer, or tablet. Participants were allowed to activate the program through any platform, but computers were recommended due to better technical optimization.

2.2.2 ASMR audio

Five relaxing tapping ASMR videos were retrieved from YouTube based on view count since the popularity could represent audience engagement and revisitation, which indicates their effectiveness in inducing ASMR. The visuals were removed to preserve only the auditory component, which was shortened to a 20-s audio clip. The same audio was shared across all conditions regardless of ASMR ability. By doing this, we examined if altering the auditory stimuli's context could affect the emotional outcome of ASMR.

2.2.3 ASMR videos

Eleven muted video stimuli were retrieved from YouTube based on their view count and congruence to the corresponding condition (fear, relaxation, and control) and auditory stimuli (tapping sounds). They were trimmed to 20 s to match the duration of the auditory stimuli. The five videos utilized for the relaxation condition were extracted from the original visuals where the ASMR audio was acquired (i.e., the visuals originated from the ASMR audio) to ensure the condition elicits the intended (positive) ASMR experience from the source material. In addition, five videos were used in the fear condition and picked based on their popularity, which we assumed indicated their capability to induce fear. These clips were obtained from horror movies and fearsome ASMR videos shared on YouTube. They were congruent to the ASMR tapping audio (e.g., raining in a forest at night, stalked by crawly monster steps, haunted house and sewer tour, and monster tapping closet; see Supplementary Appendix A) to ensure a congruent association between the audio and video. Finally, one emotionally neutral video clip was used in the control condition (a ball bouncing at a constant speed; see Supplementary Appendix A).

2.2.4 ASMR checklist

Two questions needed to be answered before proceeding to the experiment to label participants as ASMR capable or incapable: (1) Have you ever experienced ASMR? (Yes/No); (2) Which type of ASMR are you capable of (select from Whispering, Chewing, Brushing, Tapping, Scratching, & Crinkling). Participants who selected "No" for the first question or did not choose "tapping" in the second question were allocated to the "ASMR Incapable" group.

2.2.5 Self-assessment manikin scale

Self-assessment manikin scale (SAM) is a three-item pictorial assessment that measures arousal, valence, and dominance associated with an individual's emotional reaction when reacting to various stimuli (Bradley and Lang, 1994). The current experiment adapted the 9-point version of the scale, removed the dominance scale, and replaced it with an original scale that accesses ASMR intensity (1 = "No arousal"/"No ASMR"/"Extremely Unpleasant" to 9 = "Extremely aroused"/"Extreme ASMR intensity"/"Extremely Pleasant"; see

---

[1] https://www.reddit.com/r/asmr/

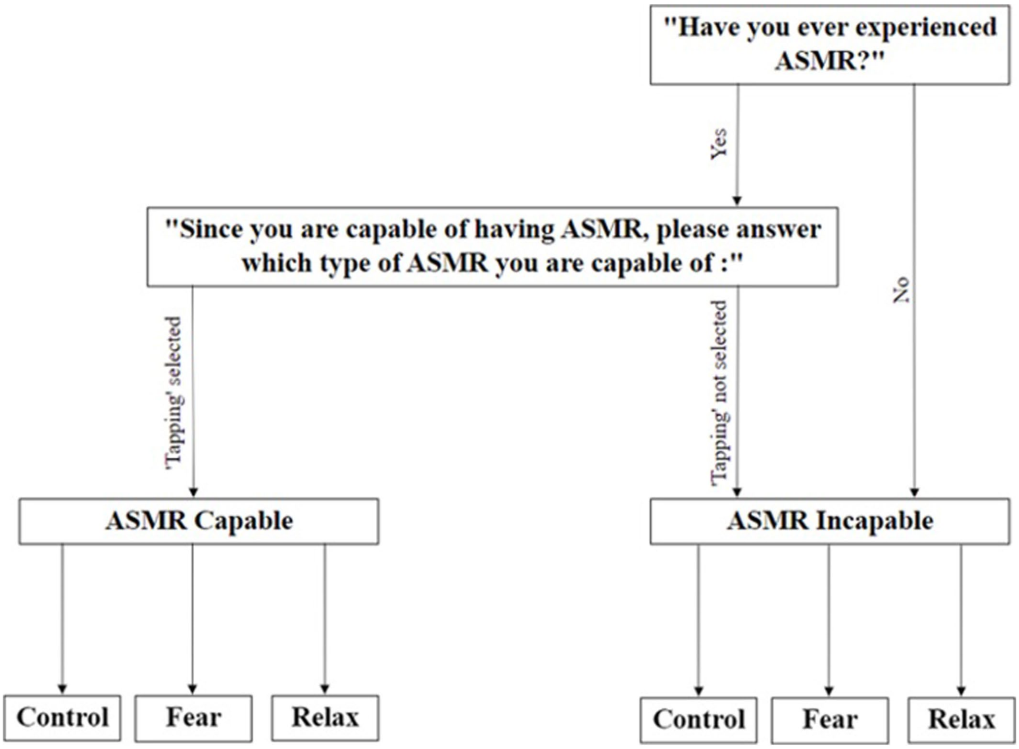


FIGURE 1
New SAM ASMR intensity scale (1=No ASMR, 9=Extreme ASMR intensity).

Supplementary Appendix B). This current assessment consisted of nine images for each scale, and each image of the scale was a visual representation of what each rating should feel like emotionally as a reference.

2.2.6 Brief mood introspection scale

This scale is an open-source 4-point Likert mood scale that contains 16 mood adjectives (Mayer and Gaschke, 1988; Lively, Happy, Sad, Tired, Caring, Content, Gloomy, Jittery, Drowsy, Grouchy, Peppy, Nervous, Calm, Loving, Fed up, and Active). Participants had to report to what extent each adjective describes their current mood (1 = "Definitely do not feel," 2 = "Do not feel," 3 = "Slightly feel," 4 = "Definitely Feel"). The data yielded were adjusted by reverse scoring components to reflect the pleasant–unpleasant mood or arousal–calm mood (Mayer and Cavallaro, 2019). Two BMIS were distributed; one was presented before the experiment, and the other was presented after the experiment. An overall pleasant–unpleasant or arousal–calm mood change score was obtained by deducting the BMIS before the experiment with the BMIS after the experiment. The reported Cronbach's alpha for the questionnaire before and after the experiment were 0.84 and 0.87 for pleasant–unpleasant and 0.42 and 0.44 for arousal–calm, respectively.

2.3 Design

The current experiment used a 2 × 3 factorial design. Independent variables were the participant's ASMR capability and the allocated priming conditions (i.e., control, fear, and relaxation). The dependent variables were (1) average SAM valence score, (2) average SAM arousal score, (3) average SAM ASMR intensity score, (4) BMIS unpleasant-pleasant mood change, and (5) BMIS arousal-calm mood change.

2.4 Procedure

2.4.1 Pre-experiment phase

Participants were given a link to the web-based experimental program. Once consent was obtained, participants completed demographic information (age, gender, and nationality) and then completed a pre-screening questionnaire to identify as either ASMR capable or incapable. They were then allocated randomly to control, relaxation, or fear conditions and were given the BMIS to measure their mood before ASMR exposure.

2.4.2 Experiment phase

Participants were then shown a muted video clip with the emotional context coherent to their grouping (i.e., neutral, relaxing, or fearsome). Once they watched the clip, participants were presented with a button to continue, which triggered a random audio clip (ASMR tapping) that lasted for another 20 s. Subsequently, participants were brought to four separate screens, where they had to provide their responses in the chronological order of (1) arousal, (2) valence, (3) ASMR intensity (see Supplementary Appendix B), and (4) interpretation of how the auditory stimulus is produced. After they completed SAM, participants were shown another muted video followed by ASMR audio, then SAM. This procedure was repeated five times; the combination of video and audio stimuli was randomly assorted for each trial and each run. All audio and video only appeared once throughout the entirety of the experiment. However, this is slightly different for the control conditions, as only one video was used as the neutral stimulus to serve as a consistent control; therefore, only the audio was randomized between trials and paired with said video.

2.4.3 Post-experiment phase

When all five trials were completed, participants were instructed to complete another BMIS to measure their overall mood after the experiment, and participants were debriefed (see Figure 2).

2.5 Data analyses

Statistical analyses were carried out using the software IBM SPSS, version 27. The analysis was separated into three stages utilizing two-way ANOVA and one-way MANOVA.

2.5.1 Analysis I

A 2 × 3 MANOVA with Bonferroni correction *post hoc* analysis is to be conducted to examine the overall differences in SAM valence, SAM arousal, SAM ASMR intensity, unpleasant–pleasant mood change, and arousal–calm mood change between ASMR capability and priming conditions. This would provide an overview of whether there will be significant main effects and interactions between the two independent variables (ASMR capability and emotional priming).

2.5.2 Analysis II

Two one-way MANOVAs with Bonferroni correction post-hoc analysis are to be conducted to compare the same dependant variables, as the first analysis between priming conditions within ASMR capable and incapable conditions separately. Examining the differences in outcomes between priming conditions within the ASMR-incapable group allows for verification of whether our visual stimuli can induce the desired emotional outcome in the absence of ASMR. In contrast, examining the ASMR capable group allows examining how ASMR intensity varies between emotions for capable individuals testing the hypotheses: (1) ASMR is a neutral physiological response that is not exclusive to inducing contentment and (2) ASMR is an emotionally neutral physiological response that is not evoked by emotion.

2.5.3 Analysis III

Three one-way ANOVA analyses will be conducted to compare dependent variables of the same priming condition between ASMR capability groups (e.g., capable fear group vs. incapable fear group). This allows examining the influence of ASMR on emotion and mood when ASMR is present compared to when it is absent. This enables us to test the hypotheses: (1) ASMR is a neutral physiological response that is not exclusive to inducing contentment, and (2) Fear-based ASMR would induce an opposite effect compared to relaxing ASMR, which increases arousal and decreases valence.

3 Results

Descriptive statistics for each group are presented in Table 1, which depicts the mean SAM arousal and valence score across all five

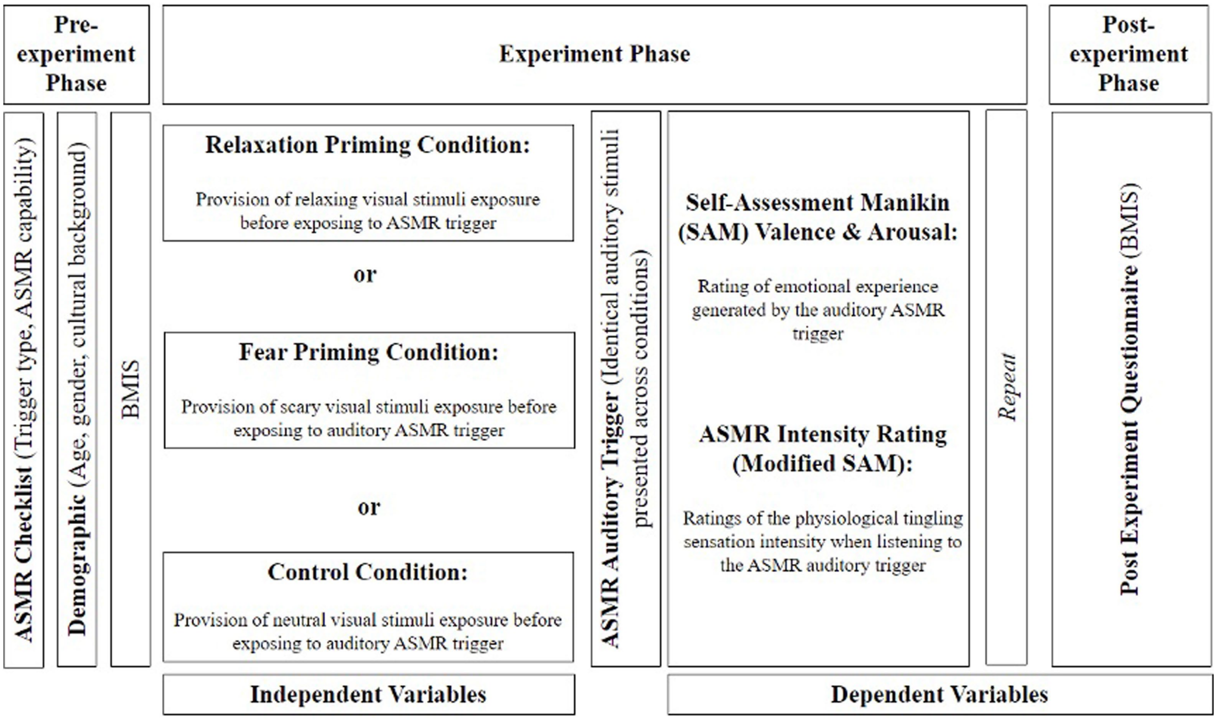


FIGURE 2
Experimental procedure.

TABLE 1 Descriptive statistic of SAM and BMIS between ASMR capability and priming conditions.

	Mean (SD)					
	ASMR Incapable (n = 51)			ASMR Capable (n = 129)		
	Control (n = 16)	Fear (n = 16)	Relaxation (n = 19)	Control (n = 50)	Fear (n = 33)	Relaxation (n = 46)
Self-assessment manikin (SAM)						
Arousal	3.13 (1.23)	4.25 (2.00)	2.78 (1.02)	3.16 (1.45)	4.58 (1.50)	3.33 (1.51)
Valence	4.83 (0.86)	4.71 (0.74)	5.41 (1.06)	5.82 (1.15)	5.10 (1.41)	6.20 (0.96)
ASMR intensity	3.51 (1.58)	3.54 (1.80)	3.01 (1.69)	4.12 (1.65)	4.52 (2.12)	4.73 (1.80)
The brief mood introspection scale (BMIS)						
Unpleasant-pleasant mood change	−1.25 (5.03)	−5.00 (6.31)	1.16 (3.20)	1.60 (4.76)	−3.45 (7.40)	2.13 (4.63)
Arousal-calm mood change	−1.25 (3.00)	1.31 (2.89)	−2.00 (2.52)	−1.04 (3.08)	0.45 (4.09)	−1.72 (2.44)

SD, standard deviation; BMIS scores are obtained by deducting pre-experiment BMIS scores with post-experiment BMIS score; The lower the unpleasant–pleasant mood change score, the more unpleasant the mood; The lower the arousal–calm mood change score, the calmer the mood.

trials, as well as unpleasant–pleasant mood change and arousal–calm mood change.

A total of 180 data points were analyzed; 51 participants were labeled as incapable of experiencing ASMR (28.3%) and 129 participants were reported to be capable of experiencing ASMR tapping (71.7%). The ASMR incapable group consisted of 16 participants in the control group (31.4%), 16 in the fear condition (31.4%), and 19 in the relaxation condition (37.3%), while the ASMR capable group consisted of 50 participants in the control condition (38.8%), 33 in the fear condition (25.6%), and 46 in the relaxation condition (35.7%). No extreme outliers were identified.

The average SAM arousal score, average SAM ASMR intensity score, average SAM valence score, BMIS unpleasant-pleasant mood change, BMIS, and arousal-calm mood change between ASMR capability group are graphically displayed as a cluster bar chart (see Figure 3).

3.1 Analysis I—main effect and interaction

A 2×3 MANOVA analysis was conducted to compare dependent variables (DV) between ASMR capability and priming conditions at a 95% confidence interval. This analysis highlighted that there are significant results within the main effect of ASMR capability [$F(5, 170) = 5.82$, $p < 0.001$; Wilk's $\Lambda = 0.854$, $\eta^2 = 0.146$], whereas univariate analysis suggested there are significant differences between ASMR intensity [$F(1, 174) = 13.64$, $p < 0.001$, $\eta^2 = 0.073$] and valence [$F(1, 174) = 15.73$, $p < 0.001$, $\eta^2 = 0.083$]. However, there was no significant differences for arousal [$F(1, 174) = 1.54$, $p = 0.22$, $\eta^2 = 0.009$] and arousal–calm mood change [$F(1, 174) = 0.06$, $p = 0.81$, $\eta^2 < 0.001$]. Although unpleasant–pleasant mood change was significant within the main effect, it showed a significant effect in Levene's test of equality of error variances, which indicated unequal variances [$F(5, 174) = 4.12$, $p < 0.05$]. Thus, Welch ANOVA will be conducted.

Moreover, a significant main effect was also found in priming conditions [$F(10, 340) = 6.36$, $p < 0.001$; Wilk's $\Lambda = 0.710$, $\eta^2 = 0.157$]. However, univariate analyses suggested that arousal [$F(2, 174) = 12.24$, $p < 0.001$, $\eta^2 = 0.123$], valence [$F(2, 174) = 8.05$, $p < 0.05$, $\eta^2 = 0.085$], and arousal–calm mood change [$F(2, 174) = 9.97$, $p < 0.001$, $\eta^2 = 0.103$] were significantly different between priming conditions except for ASMR intensity [$F(2, 174) = 0.17$, $p = 0.85$, $\eta^2 = 0.002$]. Regarding the interaction between ASMR capability and priming condition, there were no significant multivariate effect [$F(10, 340) = 0.66$, $p = 0.76$; Wilk's $\Lambda = 0.962$, $\eta^2 = 0.019$] nor differences in arousal [$F(2, 174) = 0.39$, $p = 0.68$, $\eta^2 = 0.004$], valence [$F(2, 174) = 0.90$, $p = 0.41$, $\eta^2 = 0.010$], ASMR intensity [$F(2, 174) = 1.27$, $p = 0.29$, $\eta^2 = 0.014$], and arousal–calm mood [$F(2, 174) = 0.49$, $p = 0.61$, $\eta^2 = 0.006$; see Table 2].

Post-hoc analysis on the main effect of priming conditions using Bonferroni correction tests showed that there was no significant difference in any of the dependent variables between the control and relaxation conditions. In contrast, all dependent variables except for ASMR intensity were significantly different when comparing fear against the control and relaxation conditions. Both control and relaxation had significantly higher (positive) valence, lesser arousal, lower arousal–calm mood, and higher pleasant–unpleasant mood change compared to fear (see Table 1). A lower arousal–calm mood change value refers to a calmer mood, and a higher pleasant–unpleasant mood change value refers to a more pleasant mood. There were no significant differences in ASMR intensity between all three priming conditions. Contrasts between ASMR capability, arousal, and arousal–calm mood change were not significantly different between ASMR capable and incapable samples. However, there were significantly higher levels of ASMR intensity and positive valence within the ASMR capable group than the incapable group (see Table 1).

Welch ANOVA was conducted for unpleasant–pleasant mood change due to unequal variance. This demonstrated that the ASMR capable group had significantly higher unpleasant–pleasant mood changes compared to the ASMR incapable group at $F(1, 99.27) = 4.77$, $p < 0.05$. This indicates that the ASMR capable group had a significant increase in pleasantness in mood after the experiment. Furthermore, a significant main effect of the priming condition was also found from Welch's statistics at $F(2,103.97)$, $p < 0.001$. Bonferroni post-hoc test suggested no significant differences in unpleasant–pleasant mood change between control ($M = 0.91$, $SD = 4.94$) and relaxation conditions ($M = 1.85$, $SD = 4.26$). However, the fear condition demonstrated a significantly more unpleasant mood when compared to control and relaxation ($M = -3.45$, $SD = 7.03$; see Table 2).

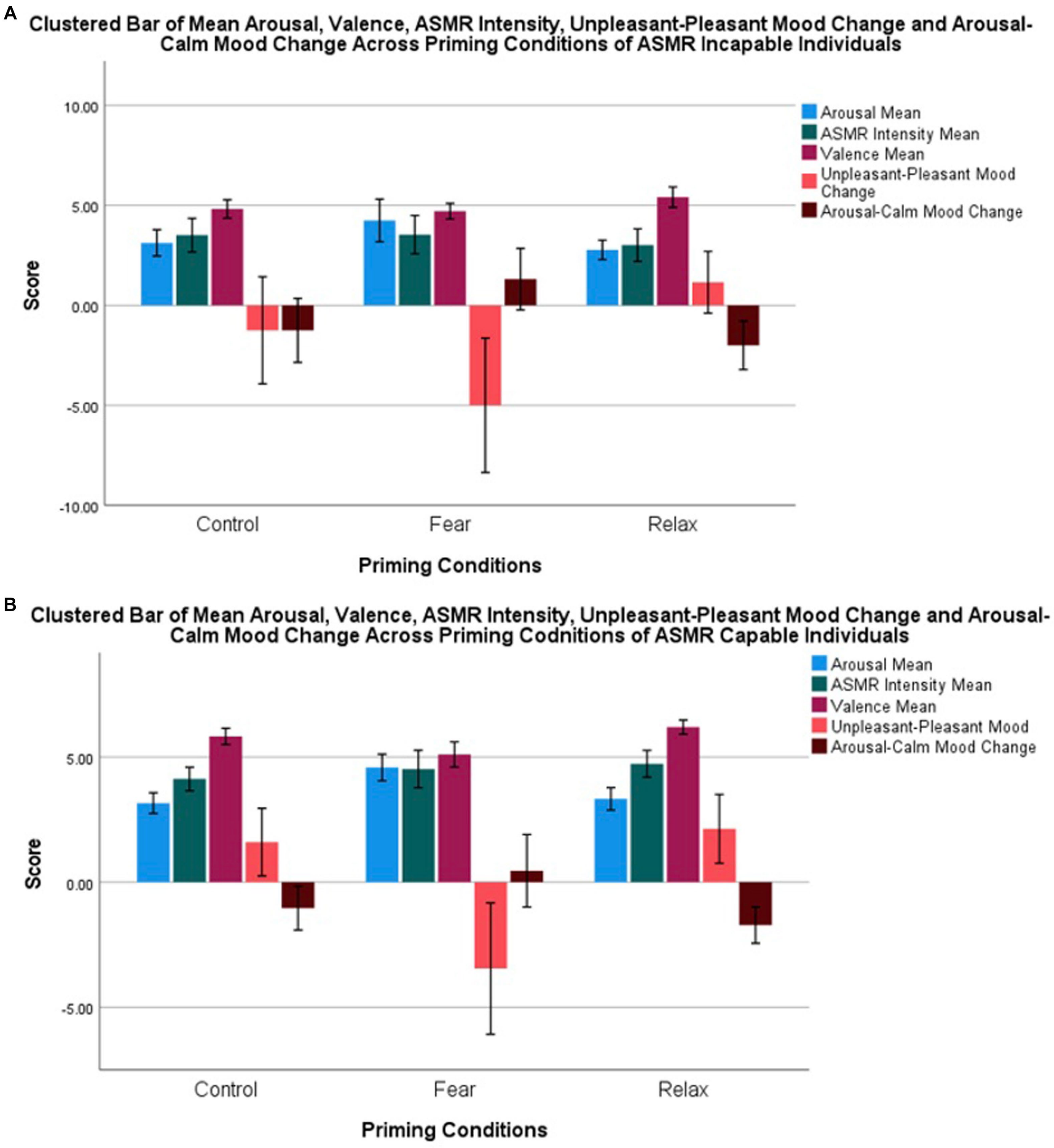


FIGURE 3
Cluster bar of mean arousal, valence, ASMR intensity, unpleasant–pleasant mood change, and arousal–calm mood changes of ASMR-incapable **(A)** and ASMR-capable individuals **(B)**.

3.2 Analysis II—ASMR capability specific between priming conditions analysis

Two one-way MANOVAs were conducted to examine how priming conditions within ASMR-capable or incapable groups differ from the other priming conditions within the same group. For the ASMR-incapable group, there were significant multivariate effects at $F(10, 88) = 2.56$, $p < 0.05$; Wilk's $\Lambda = 0.601$, $\eta^2 = 0.225$, and univariate analysis suggested significant differences for arousal–clam mood changes [$F(2, 48) = 6.52$, $p < 0.01$, $\eta^2 = 0.214$] and unpleasant–pleasant mood changes [$F(2, 48) = 6.84$, $p < 0.01$, $\eta^2 = 0.214$], and borderline significant difference with valence [$F(2, 48) = 3.04$, $p = 0.057$, $\eta^2 = 0.562$]. However, ASMR intensity demonstrated a non-significant difference at $F(2, 48) = 0.55$, $p = 0.58$, $\eta^2 = 0.022$. Furthermore, arousal scores were found significant in Levene's statistics at $F(2, 48) = 4.30$, $p < 0.05$. This indicates unequal variances, and Welsch's ANOVA was conducted, which resulted in significant differences at $F(2, 28.57) = 3.52$, $p < 0.05$. Bonferroni *post-hoc* tests suggested that there was no significant difference in arousal, arousal–calm mood change, and unpleasant–pleasant mood change between control and relaxation

TABLE 2 The 2 × 3 MANOVA analysis on main effect and interaction and Welch ANOVA on unpleasant–pleasant mood changes.

	Wilk's Λ	df	df(Error)	F	p	η^2
ASMR capability	0.854	5	170	5.82	<0.001	0.146
ASMR intensity		1	174	13.64	<0.001	0.073
Valence		1	174	15.73	<0.001	0.083
Arousal		1	174	1.54	0.22	0.009
Arousal–calm mood change		1	174	0.06	0.81	<0.001
Priming condition	0.710	10	340	6.36	<0.001	0.157
ASMR intensity		2	174	0.17	0.85	0.002
Valence		2	174	8.05	<0.05	0.085
Arousal		2	174	12.24	<0.001	0.123
Arousal–calm mood change		2	174	9.97	<0.001	0.103
ASMR capability × priming condition	0.962	10	340	0.66	0.76	0.019
ASMR intensity		2	174	0.39	0.68	0.004
Valence		2	174	0.90	0.41	0.010
Arousal		2	174	1.27	0.29	0.014
Arousal–calm mood change		2	174	0.49	0.61	0.006
Unpleasant–pleasant mood change		1	99.27	4.77	<0.05	

conditions. However, the fear condition had significantly higher arousal, aroused mood, and unpleasant mood (see Table 1) when compared to the relaxation condition. Furthermore, no significant differences were found in ASMR intensity and valence among all three conditions (see Table 3).

With regard to the ASMR capable group, arousal–calm mood change [$F(2, 126) = 4.04$, $p < 0.05$] and unpleasant–pleasant mood change [$F(2, 126) = 6.91$, $p < 0.01$] were significant in the Levene statistics. Thus, Welch ANOVA tests were carried out where unpleasant–pleasant mood change was significant at $F(2, 71.06) = 7.57$, $p < 0.01$, and arousal–calm mood changes were significant at $F(2, 71.44) = 3.77$, $p < 0.05$. Significant multivariate effect was reported at $F(10, 244) = 5.71$, $p < 0.001$; Wilk's $\Lambda = 0.657$, $\eta^2 = 0.190$. Arousal and valence were found significant at $F(2, 126) = 10.23$, $p < 0.001$, $\eta^2 = 0.140$ and $F(2, 126) = 8.59$, $p < 0.001$, $\eta^2 = 0.120$. Bonferroni post-hoc test showed no significant difference between control and relaxation conditions for all dependent variables. However, fear conditions demonstrated significantly higher arousal, negative valence, aroused mood, and unpleasant mood compared to control and relaxation, except for ASMR intensity (see Table 1), where all conditions demonstrated no significant differences (see Table 3).

3.3 Analysis III—priming conditions specific between ASMR capability analysis

Three one-way MANOVAs were conducted to compare how the same priming condition differs between ASMR capability groups. First, control conditions demonstrated a significant multivariate effect at $F(5, 60) = 0.793$, $p < 0.05$; Wilk's $\Lambda = 0.793$, $\eta^2 = 0.207$, and significant increased positive valence and pleasantness in the mood when ASMR is present at $F(1, 64) = 10.24$, $p < 0.01$, $\eta^2 = 0.138$ and $F(1, 64) = 4.23$, $p < 0.05$, $\eta^2 = 0.062$. However, no significant differences were identified for arousal [$F(1, 64) < 0.01$, $p = 0.93$, $\eta^2 < 0.001$], ASMR intensity [$F(1, 64) = 1.69$, $p = 0.20$, $\eta^2 = 0.026$], and unpleasant–pleasant mood change [$F(1, 64) = 0.06$, $p = 0.81$, $\eta^2 = 0.001$]. Second, the fear condition did not show a significant multivariate effect [$F(5, 43) = 0.85$, $p = 0.52$; Wilk's $\Lambda = 0.910$, $\eta^2 = 0.090$] nor results for all dependent variables when compared between ASMR-capable and incapable samples. However, arousal is at $F(1, 47) = 0.42$, $p = 0.52$, $\eta^2 = 0.009$, valence at $F(1, 47) = 1.07$, $p = 0.31$, $\eta^2 = 0.022$, ASMR intensity at $F(1, 47) = 2.55$, $p = 0.18$, $\eta^2 = 0.051$, unpleasant–pleasant mood change at $F(1, 47) = 0.52$, $p = 0.48$, $\eta^2 = 0.011$, and arousal–calm mood change at $F(1, 47) = 0.57$, $p = 0.46$, $\eta^2 = 0.012$. Finally, the relaxation condition showed significant multivariate effect at $F(5, 59) = 3.29$, $p < 0.05$; Wilk's $\Lambda = 0.782$, $\eta^2 = 0.218$ and demonstrated that ASMR intensity and valence were significant at $F(1, 63) = 12.65$, $p < 0.001$, $\eta^2 = 0.167$ and $F(1, 63) = 8.29$, $p < 0.01$, $\eta^2 = 0.118$, respectively. However, there were no significant results for arousal [$F(1, 63) = 2.10$, $p = 0.15$, $\eta^2 = 0.032$], unpleasant–pleasant mood change [$F(1, 63) = 0.70$, $p = 0.41$, $\eta^2 = 0.011$], and arousal–calm mood change [$F(1, 63) = 0.18$, $p = 0.68$, $\eta^2 = 0.032$]. Furthermore, arousal demonstrated significant Levene's statistics at $F(1, 63) = 5.59$, $p < 0.05$, indicating unequal variances. Regardless, Welch ANOVA showed a non-significant result for arousal at $F(1, 49.77) = 2.91$, $p = 0.094$ (see Table 4).

4 Discussion

This study employs popular YouTube videos to test the hypothesis that positive emotions are not solely determined by the ASMR sensation itself but rather by the sound that amplifies emotions triggered by visual stimuli, whether positive or negative. We demonstrate that the same ASMR tapping sound, when primed

TABLE 3 **ASMR capability specific between priming conditions MANOVA analysis.**

	Wilk's Λ	*df*	*df*(Error)	*F*	*p*	η^2
ASMR incapable	0.601	10	88	2.56	<0.05	0.225
ASMR intensity		2	48	0.55	0.58	0.022
Valence		2	48	3.04	0.057	0.562
Arousal		2	28.57	3.52	<0.05	
Arousal–calm mood change		2	48	6.52	<0.01	0.214
Unpleasant–pleasant mood change		2	48	6.84	<0.01	0.214
ASMR capable	0.657	10	244	5.71	<0.001	0.190
ASMR intensity		2	126	1.35	0.26	0.190
Valence		2	126	8.59	<0.001	0.120
Arousal		2	126	10.23	<0.001	0.140
Arousal–calm mood change		2	71.06	7.57	<0.001	
Unpleasant–pleasant mood change		2	71.44	3.77	<0.05	

TABLE 4 **Priming conditions specific between ASMR capability MANOVA analysis.**

	Wilk's Λ	*df*	*df* (Error)	*F*	*p*	η^2
Control	0.793	5	60	0.793	<0.05	0.207
ASMR intensity		1	64	1.69	0.20	0.026
Valence		1	64	10.24	<0.01	0.138
Arousal		1	64	<0.01	0.93	<0.001
Arousal–calm mood change		1	64	0.06	0.81	0.001
Unpleasant–pleasant mood change		1	64	4.23	<0.05	0.062
Fear	0.910	5	43	0.85	0.52	0.090
ASMR intensity		1	47	2.55	0.18	0.051
Valence		1	47	1.07	0.31	0.022
Arousal		1	47	0.42	0.52	0.009
Arousal–calm mood change		1	47	0.57	0.46	0.012
Unpleasant–pleasant mood change		1	47	0.52	0.48	0.011
Relaxation	0.782	5	59	32.29	<0.05	0.218
ASMR intensity		1	63	12.65	<0.001	0.167
Valence		1	63	8.29	<0.01	0.032
Arousal		1	49.77	2.91	0.09	
Arousal–calm mood change		1	63	0.70	0.41	0.011
Unpleasant–pleasant mood change		1	63	0.18	0.68	0.032

with videos of different emotional valences (fear, relaxation, and control), elicits an amplification effect on subjects, particularly those who are ASMR-capable.

As predicted, fear-based ASMR increased arousal and decreased positive valence compared to relaxation-based ASMR. Although the role of ASMR in a fearful context might require further testing, the results demonstrated that ASMR occurs also under non-relaxed experience. The sensation itself is not responsible for determining the emotional outcome, but it could possibly serve as a physical amplifier of the emotion appraised. If ASMR was a response that was always accompanied by relaxation, fear priming should not have had the effect of reducing positive valence and increasing arousal. The level of ASMR intensity does not significantly differ across priming conditions. This indicates that the difference in emotional outcome is not caused by the absence of ASMR tingling sensation but rather by the emotion perceived in the context.

Meanwhile, both control and relaxation conditions demonstrated significant increases in valence for ASMR-capable individuals, which aligns with our assumption that ASMR acts as a medium that physically amplifies pre-existing emotions since individuals who are ASMR-capable demonstrated the same emotional score direction as ASMR-incapable individuals but to a greater extent.

The study adds its findings to the debate of whether ASMR is, in fact, the same phenomenon as frisson. In the literature, we have seen that it is inherently difficult to distinguish the physiological sensations between ASMR and frisson, with a sensation of contentment being the only differentiator highlighted so far. Thus, being able to feel ASMR in both positive and negative emotional contexts supports the idea that the two might be descriptions of the same phenomenon.

4.1 Alternative interpretations, limitations, and future directions

There is a non-significant difference between control and relaxation priming conditions for ASMR-capable individuals, which could also be evidence of bias in the ASMR community. As Smith and Snider (2019) showcased the community's encouragement toward the view of ASMR as a relaxation-based sensation, this mainstream impression of ASMR would ultimately provide enough context needed to determine the initial emotion. Subsequently, the capable control group may have decided to anticipate ASMR as a relaxing response, which amplifies their contentment. This could explain the non-significant differences between control and relaxation conditions.

One could interpret the effect induced by fear-based ASMR as suppression of contentment induction when interpreting stimuli negatively. To elaborate further, while the relaxation condition demonstrated that the presence of ASMR leads to improved valence, this effect is absent in the fear condition as none of the dependent variables have shown to be significantly different between the capable and incapable groups. This valence-improving effect in the relaxation condition seems suppressed under a fear-related context. If this is the case, the result would indicate that there is a certain threshold before ASMR becomes ineffective in inducing contentment, which may be an exciting aspect for future investigations wanting to explore the parameters of ASMR as a therapeutic or meditative medium.

Although the results might favor the suppression theory since there were no significant differences in emotions across ASMR capability groups in the fear condition, it is possible that the amplification hypothesis still stands due to a response bias. This assumes that most ASMR-incapable individuals do not know what ASMR-tapping feels like and resort to central tendency bias to avoid giving extreme responses, which causes the non-significant statistics between fear-incapable and capable groups. This is supported by no significant differences in ASMR intensity for the fear priming conditions between ASMR capability groups. Similarly, ASMR intensity does not significantly differ between capability groups for the control condition. We can assume that the problem does not arise from the ASMR capable group since both priming conditions shared the same level of ASMR intensity with the capable relaxation group, which was statistically different than its incapable counterparts. Overall, some non-significant ASMR intensity differences found between the capabilities group (i.e., fear and control conditions) and the average ASMR intensity score in the incapable group being over three points are assumed to be caused by response bias. Regardless, the main effect of ASMR capability on ASMR intensity score remains statistically significant, which indicates that the capability groups are sufficiently different for the analyses.

To confirm and eliminate our suspicion of response bias at play, future research could adapt new baselines with ASMR-capable individuals who would go through the same priming procedure but do not receive auditory ASMR stimulation to eliminate the possibility of experiencing ASMR as part of the ASMR-incapable group (control group). Future incorporation of personality traits measurements may also be useful for sanity checking for grouping errors between ASMR capability groups, as ASMR-capable individuals have shown to have significantly higher scores on openness-to-experience and neuroticism but significantly lower levels of conscientiousness, extraversion, and agreeableness (e.g., Fredborg et al., 2017; McErlean and Banissy, 2017).

Alternatively, more direct measurements could be implemented to investigate fear-related ASMR to counteract questionnaire biases. For instance, fMRI (Smith et al., 2019) or EEG (Fredborg et al., 2021) was used to examine areas such as the right cingulate gyrus, right paracentral lobule, and bilateral thalamus that indicate ASMR experience to ensure appropriate and more precise groupings of ASMR-capable and incapable individuals for better clarity of the true effect with fear-related ASMR when comparing affective differences across capability groups.

Furthermore, measurement errors caused by equipment differences among participants may be present. Since the investigation was conducted online, we had no control over the monitor size or auditory apparatus utilized, and participants' different monitors or headphones might have influenced their perception of the auditory stimuli or priming material, which in turn may have influenced their emotional ratings. Regarding the perception of auditory stimuli, Koumura et al. (2020) have suggested that the intensity of the frisson-like sensation from ASMR is linked to the acoustic features of the auditory stimuli, such as amplitude, spectral centroid, and spectral bandwidth. The lack of control in audio devices could influence the perceptibility of acoustic components; subsequently, failing to perceive acoustic intricacies could disable the initiation of the ASMR experience. However, significantly higher ASMR intensity for capable individuals would indicate the presence of ASMR, which further implies that participants were able to perceive our auditory material appropriately and that the effect of equipment variance did not significantly impact the results.

Future research could objectively investigate whether ASMR is a susceptibility in physiological response that causes one to be extra sensitive toward certain auditory stimuli, which is independent of emotions. This is not unlike those who are more sensitive to skin contact and are labeled as "ticklish." Translating this into the context of ASMR, ASMR-capable individuals may simply be more sensitive to a certain pitch, sound patterns, tone, or other auditory properties of the ASMR trigger, which leads to a physical response to the extra sensitivity.

5 Conclusion

In conclusion, ASMR was shown to be present under different emotional states, suggesting that the effect of ASMR can be altered by influencing the affective interpretation of ASMR stimuli, supporting the idea that, similar to frisson, it is a physically amplified, overwhelming emotional experience. With relaxation-based ASMR, the tingling sensations may serve as an amplifier to boost the pre-existing contentment. In contrast, fear-based ASMR seems to suppress contentment induction when the stimuli are interpreted negatively, and significantly higher arousal and negative valence are induced by attaching a fearful context to ASMR stimuli, showing that ASMR does not always induce relaxation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by the University College London, Department of Information Study Ethics Chair. The participants provided their informed consent to participate in this study online. The studies were conducted in accordance with the local legislation and institutional requirements.

Author contributions

WLL and DR: writing, review and editing, data curation, formal analysis, and investigation. WLL: data collection and literature review. DR: research supervision. All authors contributed to the article and approved the submitted version.

Funding

Funding for the participants' vouchers was provided by the Department of Psychology and Language Sciences, University College London, United Kingdom.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2024.1183996/full#supplementary-material

References

Ahuja, A., and Ahuja, N. K. (2019). Clinical role-play in autonomous sensory meridian response (ASMR) videos: performance and placebo in the digital era. *JAMA* 321, 1336–1337. doi: 10.1001/jama.2019.2302

Andersen, J. (2015). Now you've got the shiveries: affect, intimacy, and the ASMR whisper community. *Telev. New Media* 16, 683–700. doi: 10.1177/1527476414556184

Barratt, E. L., and Davis, N. J. (2015). Autonomous sensory Meridian response (ASMR): a flow-like mental state. *Peer J* 3:e851. doi: 10.7717/peerj.851

Barratt, E. L., Spence, C., and Davis, N. J. (2017). Sensory determinants of the autonomous sensory meridian response (ASMR): understanding the triggers. *Peer J* 5:e3846.

Benedek, M., and Kaernbach, C. (2011). Physiological correlates and emotional specificity of human piloerection. *Biol. Psychol.* 86, 320–329. doi: 10.1016/j.biopsycho.2010.12.012

Bishop, S. R., Lau, M., Shapiro, S., Carlson, L., Anderson, N. D., Carmody, J., et al. (2004). Mindfulness: a proposed operational definition. *Clin. Psychol. Sci. Pract.* 11, 230–241. doi: 10.1093/clipsy.bph077

Blood, A. J., and Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. U. S. A.* 98, 11818–11823. doi: 10.1073/pnas.191355898

Bradley, M. M., and Lang, P. J. (1994). Measuring emotion: the self-assessment manikin and the semantic differential. *J. Behav. Ther. Exp. Psychiatry* 25, 49–59. doi: 10.1016/0005-7916(94)90063-9

Cash, D. K., Heisick, L. L., and Papesh, M. H. (2018). Expectancy effects in the autonomous sensory meridian response. *Peer J* 6:e5229. doi: 10.7717/peerj.5229

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Colver, M. C., and El-Alayli, A. (2016). Getting aesthetic chills from music: the connection between openness to experience and frisson. *Psychol. Music* 44, 413–427. doi: 10.1177/0305735615572358

Del Campo, M. A., and Kehle, T. J. (2016). Autonomous sensory meridian response (ASMR) and frisson: mindfully induced sensory phenomena that promote happiness. *Int. J. Sch. Educ. Psychol.* 4, 99–105. doi: 10.1080/21683603.2016.1130582

Diamond-Flower. (2018). *Eating ASMR*. Available at: https://www.reddit.com/r/rant/comments/94ndus/eating_asmr/ (Accessed February 11, 2023).

Edelstein, M., Monk, B., Ramachandran, V. S., and Rouw, R. (2020). Context influences how individuals with misophonia respond to sounds. *BioRxiv*, 2020–2009. doi: 10.1101/2020.09.12.292391

Fairyington, S. (2014). *Rustle, tingle, relax: the compelling world of ASMR* The New York Times.

Faul, F., Erdfelder, E., Lang, A.-G., and Buchner, A. (2007). G*power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Methods* 39, 175–191. doi: 10.3758/BF03193146

Fredborg, B. K., Champagne-Jorgensen, K., Desroches, A. S., and Smith, S. D. (2021). An electroencephalographic examination of the autonomous sensory meridian response (ASMR). *Conscious. Cogn.* 87:103053. doi: 10.1016/j.concog.2020.103053

Fredborg, B., Clark, J., and Smith, S. D. (2017). An examination of personality traits associated with autonomous sensory meridian response (ASMR). *Front. Psychol.* 8:247. doi: 10.3389/fpsyg.2017.00247

Fredborg, B., Clark, J., and Smith, S. D. (2018). Mindfulness and autonomous sensory meridian response (ASMR). *Peer J.* 6:e5414. doi: 10.7717/peerj.5414

Grewe, O., Kopiez, R., and Altenmüller, E. (2009). The chill parameter: goose bumps and shivers as promising measures in emotion research. *Music. Percept.* 27, 61–74. doi: 10.1525/mp.2009.27.1.61

Gu, S., Wang, F., Patel, N. P., Bourgeois, J. A., and Huang, J. H. (2019). A model for basic emotions using observations of behavior in Drosophila. *Front. Psychol.* 10:781. doi: 10.3389/fpsyg.2019.00781

Guhn, M., Hamm, A., and Zentner, M. (2007). Physiological and musico-acoustic correlates of the chill response. *Music. Percept.* 24, 473–484. doi: 10.1525/mp.2007.24.5.473

I Started to Notice. (2016). *Anyone else experience asmr from fear or really bad tasting things e.g pure caffeine? [online]*. Available at: https://www.reddit.com/r/asmr/comments/43l61q/question_anyone_else_experience_asmr_from_fear_or/ (Accessed October 30, 2023).

ima-lick-u. (2018). *ASMR with food is disgusting*. Available at: https://www.reddit.com/r/unpopularopinion/comments/9y8gst/asmr_with_food_is_disgusting/?rdt=58930 (Accessed February 11, 2023).

Koumura, T., Nakatani, M., Liao, H. -I., and Kondo, H. M. (2020). Dark, loud, and compact sounds induce frisson. *Q. J. Exp. Psychol.* 74, 1140–1152. doi: 10.1177/1747021820977174

Kovacevich, A., and Huron, D. (2018). Two studies of autonomous sensory meridian response (ASMR): the relationship between ASMR and music-induced frisson. *Empir. Musicol. Rev.* 13, 39–63. doi: 10.18061/emr.v13i1-2.6012

Kovacevich, A., and Huron, D. (2019). Two studies of autonomous sensory meridian response (ASMR): the relationship between ASMR and music-induced frisson. *Empir. Musicol. Rev.* 13:39.

Lohaus, T., Yüksekdag, S., Bellingrath, S., and Thoma, P. (2023). The effects of autonomous sensory Meridian response (ASMR) videos versus walking tour videos on ASMR experience, positive affect and state relaxation. *PLoS One* 18:e0277990. doi: 10.1371/journal.pone.0277990

Lutz, A., Slagter, H. A., Dunne, J. D., and Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends Cogn. Sci.* 12, 163–169. doi: 10.1016/j.tics.2008.01.005

Mayer, J. D., and Cavallaro, R. (2019). Brief mood introspection scale (BMIS): Technical and scoring manual.

Mayer, J. D., and Gaschke, Y. N. (1988). The experience and meta-experience of mood. *J. Pers. Soc. Psychol.* 55, 102–111. doi: 10.1037/0022-3514.55.1.102

McErlean, A. B. J., and Banissy, M. J. (2017). Assessing individual variation in personality and empathy traits in self-reported autonomous sensory meridian response. *Multisens. Res.* 30, 601–613. doi: 10.1163/22134808-00002571

McGinn, C., and Kelly, K. (2018). "Using the Geneva emotion wheel to classify the expression of emotion on robots" in *Companion of the 2018 ACM/IEEE International Conference on Human-Robot Interaction*, 191–192.

Panksepp, J. (1995). The emotional sources of" chills" induced by music. *Music. Percept.* 13, 171–207. doi: 10.2307/40285693

Pittig, A., Arch, J. J., Lam, C. W., and Craske, M. G. (2013). Heart rate and heart rate variability in panic, social anxiety, obsessive–compulsive, and generalized anxiety disorders at baseline and in response to relaxation and hyperventilation. *Int. J. Psychophysiol.* 87, 19–27. doi: 10.1016/j.ijpsycho.2012.10.012

Poerio, G. L., Blakey, E., Hostler, T. J., and Veltri, T. (2018). More than a feeling: autonomous sensory meridian response (ASMR) is characterized by reliable changes in affect and physiology. *PLoS One* 13:e0196645. doi: 10.1371/journal.pone.0196645

Poerio, G., Ueda, M., and Kondo, H. M. (2022). Similar but different: high prevalence of synesthesia in autonomous sensory meridian response (ASMR). *Front. Psychol.* 13:990565. doi: 10.21203/rs.3.rs-1414172/v1

Rambalac (2018). *【4K】walking at night in Aokigahara forest (no pranks, not scary. ASMR?) [video]. YouTube.* Available at: https://www.youtube.com/watch?v=hqsQY-QXI2U (Accessed October 30, 2023).

Rouw, R., and Erfanian, M. (2018). A large-scale study of misophonia. *J. Clin. Psychol.* 74, 453–479. doi: 10.1002/jclp.22500

Smejka, T., and Wiggs, L. (2022). The effects of autonomous sensory Meridian response (ASMR) videos on arousal and mood in adults with and without depression and insomnia. *J. Affect. Disord.* 301, 60–67. doi: 10.1016/j.jad.2021.12.015

Smith, S. D., Fredborg, B. K., and Kornelsen, J. (2019). A functional magnetic resonance imaging investigation of the autonomous sensory meridian response. *PeerJ* 7:e7122. doi: 10.7717/peerj.7122

Smith, N., and Snider, A. M. (2019). ASMR, affect and digitally-mediated intimacy. *Emot. Space Soc.* 30, 41–48. doi: 10.1016/j.emospa.2018.11.002

Wu, M. S., Lewin, A. B., Murphy, T. K., and Storch, E. A. (2014). Misophonia: incidence, phenomenology, and clinical correlates in an undergraduate student sample. *J. Clin. Psychol.* 70, 994–1007. doi: 10.1002/jclp.22098

Wulfert, E., Roland, B. D., Hartley, J., Wang, N., and Franco, C. (2005). Heart rate arousal and excitement in gambling: winners versus losers. *Psychol. Addict. Behav.* 19, 311–316. doi: 10.1037/0893-164X.19.3.311

Frontiers in Psychology

TYPE Review
PUBLISHED 08 March 2024
DOI 10.3389/fpsyg.2023.1260814

Empathy and the art of Leonardo da Vinci

Samira Schultz Mansur[1]* and Javier DeFelipe[2,3]

[1]Department of Morphological Sciences, Biological Science Center, Federal University of Santa Catarina, Florianópolis, Brazil, [2]Laboratorio Cajal de Circuitos Corticales, Centro de Tecnología Biomédica, Universidad Politécnica de Madrid, Madrid, Spain, [3]Instituto Cajal, Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain

EDITED BY
Andrew Kemp,
Swansea University, United Kingdom

REVIEWED BY
Piotr Oleś,
The John Paul II Catholic University of Lublin, Poland
Despina Stamatopoulou,
University of Crete, Greece

*CORRESPONDENCE
Samira Schultz Mansur
✉ samira.mansur@ufsc.br

RECEIVED 18 July 2023
ACCEPTED 21 November 2023
PUBLISHED 08 March 2024

CITATION
Mansur SS and DeFelipe J (2024) Empathy and the art of Leonardo da Vinci.
Front. Psychol. 14:1260814.
doi: 10.3389/fpsyg.2023.1260814

Knowledge about empathy is part of the study of artistic expressions, among which stand out works of personalities such as the Renaissance polymath Leonardo da Vinci, who was concerned with the connection between science and art during his creative research full of imagination and sensitivity to nature and human anatomy. The word empathy emerged among critics of German art as the term *einfühlung*, which was used within the aesthetic bias by philosophers and art historians. It emphasized the idea that a viewer perceiving an object could establish a link between it and themselves, projecting the object 'into themselves'. That is, the artwork could be experienced by the observer as if the viewer belonged predominantly to the object, in such a way that its characteristics could be actually felt through the expression of emotions, feelings and thoughts. This analysis of art appreciation required a great deal of knowledge and contemplation of nature, as understood by the German Romanticists, who had enormous admiration for da Vinci and his universal and systematic mind—a mind which reacted against formalisms, building his intellectual and sensory systems based on both his observation of nature and his own criteria. In particular, the art of painting for Leonardo was a way to demonstrate a mental discourse, just as the most important aspect of human portraits is to represent—in gestures and facial expressions—the states of mind and emotions. These are facts that German Romanticists tried to explain as the relationship between empathy and a work of art. The present manuscript aims to describe empathy from an artistic view, considering the roots of this word in German Romanticism; to comment about Leonardo da Vinci and the expression of art in the Renaissance; and, finally, to discuss the expression of his art in relation to empathy.

KEYWORDS
cognitive and emotional relationships, narrative image, artistic expression, German Romanticism, renaissance art

> "Whoever flatters himself that he can retain in his memory all the effects of Nature, is deceived, for our memory is not so capacious; therefore, consult Nature for everything" - Miscellaneous observations, That a Man ought not to trust to himself, but ought to consult Nature, c. 365 (Da Vinci, 2014, p. 208).

Introduction

Leonardo da Vinci (15 April 1452–2 May 1519) was born in Anchiano, a village near the small town of Vinci, in the period of the Italian Renaissance, in a dynamic society during a time of great intellectual awakening, transformation and resurgence of life and arts and definitive rupture of the medieval conception of the world (McMurrich, 1930, p. 3; Clark, 1976, p. 18). Leonardo is one of the greatest geniuses and polymaths to have ever existed. His work, which is shrouded in mystery, has been the subject of numerous studies in various fields of science, art, and the humanities, and has had an important impact on each of these fields.

In neuroscience, da Vinci was one of the pioneers in trying to explain in detail by physical laws how the brain processes visual information and other sensory stimuli and integrates this information "through the soul." Da Vinci believed that the anatomical visual system played an essential role in artistic perception and developed a mechanistic model based on the ventricular or cellular doctrine of brain functions (e.g., Pevsner, 2002; DeFelipe, 2017). Shown on the left of Figure 1 is the famous drawing by da Vinci of the central nervous system and cranial nerves, which were believed to be hollow and capable of transmitting "animal or generating forces." On the right of this figure, a schematic drawing of the human central nervous system by Lewellys Barker (1867–1943) is shown (Barker, 1899). This is a good example of the influence of the anatomical/functional drawings of da Vinci in the early illustrations of 'modern' neurological anatomy.

In the present article, we have focused on an extraordinary facet of this genius, namely, the expression of empathy in his artistic works. This is exemplified by the "Madonnas," which reveal his great ability to illustrate the cognitive and emotional relationships of the characters in his paintings — both between the characters themselves and with the viewer. The first paintings attributed to Leonardo show the use of the traditional disciplines of drawing, perspective and anatomy, as well as a special attention to the effects of light and nature — attention that begins to give rise to the style with which Leonardo renews the Florentine pictorial panorama and manifested in the atmospheric landscapes of works, as in the shadings that give relief to forms, especially intense, in The Virgin with the Child, called Benois Madonna (Sureda, 1998, p. 200; Figure 2). In this regard, da Vinci told his students and disciples (Landrus, 2006, p. 15):

> Decide freely on the arrangement of the figures, but always keep in mind that the movements are the expression of the desire of their mind.

The objectives of this manuscript are to explore empathy from an artistic perspective. This exploration begins with a general introduction to empathy and the works of Leonardo da Vinci. A subsequent section will address the word's roots in German Romanticism, followed by a section dealing with da Vinci and the expression of art during the Renaissance. Finally, a concluding section will discuss the expression of his art in relation to empathy.

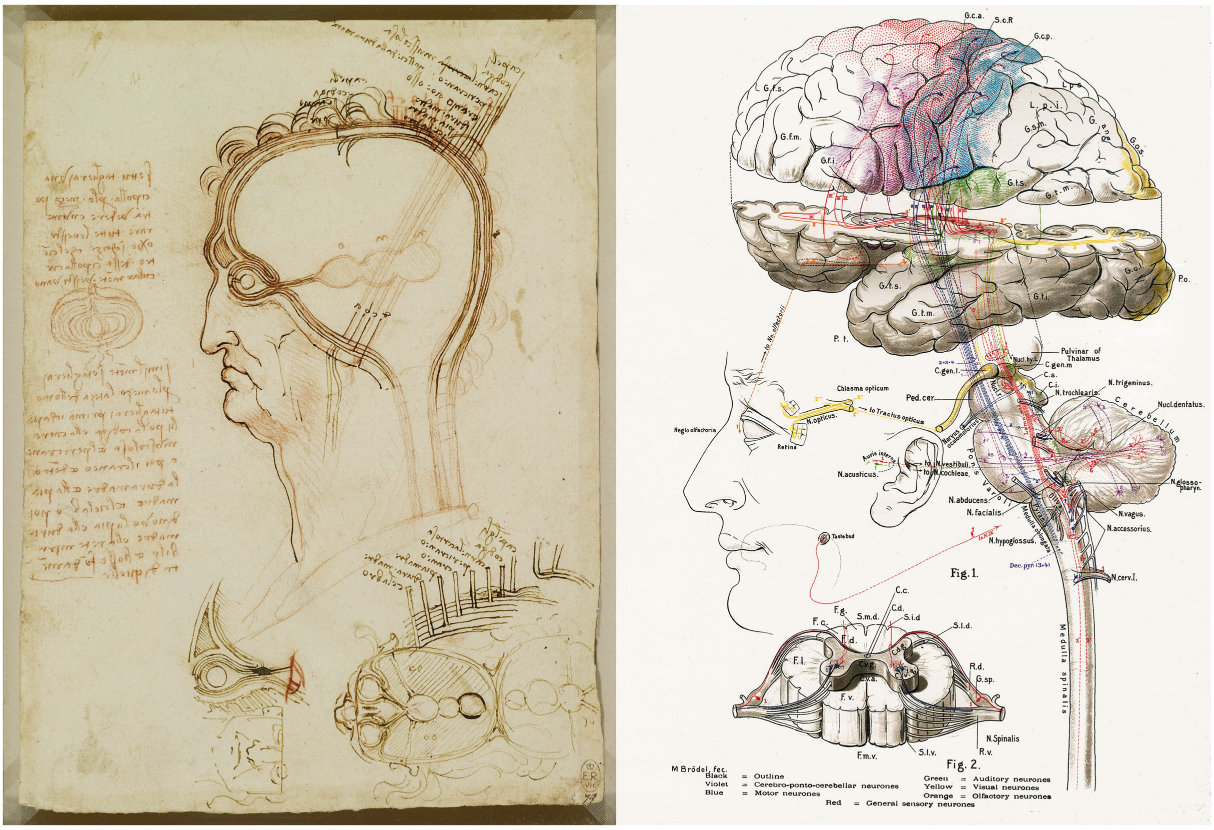


FIGURE 1
(Left) Leonardo da Vinci, *Quaderni d'anatomia* (1490): the central nervous system and cranial nerves. The main drawing shows the layers covering the brain compared to the layers of an onion cut in half (on the left of the image). At the bottom of the drawing, the ventricles viewed from above are illustrated, including the optic and auditory nerves entering the anterior ventricle. Royal Collection Trust/© His Majesty King Charles III, 2023. **(Right)** Barker (1899): schematic drawing to illustrate some of the multiple relationships between different parts of the human central nervous system. Taken from DeFelipe (2017).

FIGURE 2
Leonardo da Vinci's Benois Madonna (circa 1478). Reproduced from rawpixel via Wikimedia Commons, licenced under CC0.

Empathy and Leonardo

Empathy involves experiencing emotion vicariously and understanding the reasons for those emotions (Braadbaart et al., 2014). It may be defined as the capacity to understand other people's feelings and respond to them appropriately, though it is also considered to be a multifaceted concept that relies on cognition, emotional reactivity and social skills (Baron-Cohen and Wheelwright, 2004; Decety, 2011), while also being based on both perception and understanding (Muncer and Ling, 2006).

As highly social species, we attempt to coordinate our actions and assure successful communication by using language skills and social abilities such as empathy to infer another person's emotions and mental state (Singer and Klimecki, 2014). Among his many skills and sensibilities, Leonardo da Vinci had the ability to find —through visual language— an important way to communicate his human perceptions and expressions and represent them through art (Vecce, 2003, p. 61; Ruiz García, 2011, p. 225) in which he transmitted figuratively his mental construction about the deep observation of thoughts and emotions, translated by the intention of the mind (Bongioanni, 1978, p. 184; Kemp and Wallace, 2000, p. 16).

Empathy may be served partly by a motor simulation function, and therefore share a neural basis with imitation, as both involve sensorimotor representations of intentions based on perceptions of others' actions, as well as imagination, after which intentionality and action planning evolve (Braadbaart et al., 2014). One of the characteristics of Leonardo's way of thinking was based on analogies which were demonstrated in his figures and expressed not only a complement of a text, but an instrument that can stand alone due to its capacity to express rational thought and feelings (Cortes, 1994, p. 37; Ramón, 2011, p. 69). That is, the picture may share an empathic attitude (Titchener, 1909, p. 185) — and, within Leonardo's drawings, we always find his profound imagination and creativity linked to his systematic observation of nature (Kemp, 2003, p. 147; Capra, 2011, p. 63; Ruiz García, 2011, p. 216).

It is important to note that one of the clearly connected processes in individual brains to phenomena of interest to the humanities relies on the development of studies that potentially dissociate two systems for empathy in the brain, namely, emotional ("I feel what you feel") and cognitive ("I understand what you feel"), to examine how different empathic responses may be generated, for example, by art (Carew and Ramaswami, 2020). With regard to the drawings of Leonardo, his aim was to clearly consider the relationship between the artist's expression and the viewer of the artwork (Vecce, 2003, p. 69); for instance, he mentioned that the attitudes and all the posture in a painting ought to correspond with the sentiment expressed in the faces (Da Vinci, 2014, p. 86).

Leonardo was a pioneer in demonstrating what was possible with anatomical illustrations and his approach inspired other artists to encourage the viewer to become a witness of what he saw (Kemp and Wallace, 2000, p. 33). In this regard, he affirmed that the painted figures should be created so that the observer could easily know—through the movements and attitude of the figures—the mental situation of the creator of the narrative and the meaning of his intentions (Da Vinci, 2013, p. 121), since an experiencer must empathize with an observer in order to think, understand and communicate as he does (Titchener, 1909, p. 185).

Most of the themes presented in this introduction are expanded upon in the last chapter of this manuscript, entitled Leonardo, empathy and the expression of his art. The following sections include an essay on empathy from an artistic perspective, considering the roots of this word in German Romanticism, followed by a commentary on da Vinci and the expression of art in the Renaissance — and, finally, a discussion of the expression of his art in relation to empathy.

Empathy and German romanticism

> "One painter ought never to imitate the manner of any other; because in that case he cannot be called the child of Nature, but the grandchild. It is always best to have recourse to Nature, which is replete with such abundance of objects, than to the productions of other masters, who learnt everything from her" - Miscellaneous observations, Painters are not to imitate one another, c. 354 (Da Vinci, 2014, p. 203).

The word empathy has its roots in the Greek '*empatheia*' ('*en*', in; and '*pathos*', feeling). This term was introduced in the aesthetics of German art from the translation of the word *einfühlung*, or "feeling into," to English by the Anglo-American Edward Titchener (1867–1927), in 1909 (Stueber, 2013). The term *einfühlung* was used within an aesthetic context by the philosopher Rudolf Lotze (1817–1881) in

1858, who discovered the projection of our inner experience into forms, leading to us sharing their essence (Lee and Anstructer-Thomson, 1912, p. 17). Similarly, in 1873, the term was also used by the art historian and philosopher Robert Vischer (1847–1933), whose ideas —which were widely accepted by art historians— included the projection of himself into the artistic object (Preston and De Wall, 2002, p. 1). In his words, "I can think my way into [an object], mediate its size with my own, stretch and expand, bend and confine myself to it" (Vischer, 1873, p. 104). By *einfühlung*, Vischer meant the physical responses that are generated by the observation of paintings and he described how particular forms aroused particular responsive feelings, depending on their conformity to the design and function of the muscles of the body (Freedberg and Gallese, 2017, p. 198).

Developing Vischer's ideas, the art historian Heinrich Wölfflin (1864–1945), in 1886, set out his views on how observation of specific architectural forms engages the beholders' bodily responses, while Karl Gross (1861–1946), in 1892, used Vischer's understanding to represent aesthetic satisfaction as an activity of inner imitation (Freedberg and Gallese, 2017, p. 198). Wölfflin agreed that we subject all objects to "soulification" in this projective way, and suggested that such projection involved actual workings of the motor nerve system (Peacocke, 2023). Around the same time, Bernard Berenson (1865–1959) outlined his views on how observation of the movements shown in Renaissance works of art enhanced the beholders' sense of the capacities of the comparable muscles within their bodies (1909, p. 25). However, there were similar descriptions previously; for example, in 1774 the philosopher and novelist Johann Herder (1744–1803) associated the word in German with enlightenment to understand other times and cultures (Zölzer and Zölzer, 2020, p. 2).

Empathy among critics of German Romantic art is taken to entail aesthetic taste being an objectification of one's own personal taste, and in particular, taste for a work of art is the contemplation of an object, consisting of perceiving the vitality of this object, as the symbol of a life that is there (Lipps, 1924, p. 96). From this perspective, critical analysis of art among romanticists implies having knowledge of the object on which the work is based, with knowledge of nature considered essential (Lipps, 1924, p. 13). In turn, the object becomes a potential source of free thinking, preceded by spontaneity and knowledge, in such a way that it translates a reflection of oneself (Benjamin, 2017, p. 66) and an interpretation of the external world that mirrors the characteristic of each individual mind (DeFelipe, 2014, p. 67). Da Vinci expands on this notion as follows (from Linear Perspectives, in Of Mental Motions, c. 110; Da Vinci, 2014, p. 48):

> "A mere thought, or operation of the mind, excites only simple and easy motions of the body; not this way, and that way, because its object is in the mind, which does not affect the senses when it is collected within itself."

However, between 1903 and 1906, psychologists attributed to the German Theodor Lipps (1851–1914) the discovery of empathy, related to the German word *einfühlung*, since it was he who organized and founded the term for the area of psychology (Stueber, 2013). Lipps first proposed that empathy described the relationship between a work of art and its observer, but soon expanded this concept to encompass interactions between people by interpreting that our perception of the movements of others is a form of inner imitation (Iacoboni, 2009, p. 111). He attributed our capacity for empathy to a sensory-motor mirroring — an involuntary, kinesthetic inner imitation of the observed that informs our experience of art (Stamatopoulou, 2018, p. 170). Empathy theorists took it that aesthetic experience involved mentally projecting ourselves into the physical shape of an item to have an emotional or dynamic experience of the kind that a human subject would have if taking on that physical shape (Vischer, 1873, p. 104).

Another German, Antonin Prandtl (1880–1927), less well known than Lipps, explained —in 1910— that even though people can only know their own inner life, what is only known is the very image or thought, while understanding of the other's life can occur through empirical empathy or via empathy through feeling (Cortes, 1994, p. 30). Empirical empathy depends on a previous occurrence of feeling and assumes that it has already been felt by the person himself; empathy through feeling is closer to the version expounded by Lipps. In both types of empathy, there is the characteristic that what occurs in the viewer is driven by the object, whether it is another person or a work of art (Cortes, 1994, p. 30).

Lipps and Prandtl, among others, used the term empathy to explain how a person grasped the meaning of aesthetic objects and the consciousness of other people. Titchener, employing the term empathy, thought that one could not know the consciousness of another person trying to enter their mind through reason, but through inner imitation or motor mimicry, with an effort of the mind (1909, p. 185), which most people did to detect their 'core' of empathy. He adapted William James's (1842–1910) notion of ideomotor action—through which mental representations are scaffolded by embodied percepts—to claim that kinesthetic imagery supports empathy (Stamatopoulou, 2018, p. 170). In fact, through imitation and mimicry, we can feel what other people feel and also understand their emotional states (Iacoboni, 2009, p. 116). In this regard, Titchener wrote (Titchener, 1909, p. 21):

> "… the various visual images, which I have referred to as possible vehicles of logical meaning, oftentimes share their task with kinesthesis. Not only do I see gravity and modesty and pride and courtesy and stateliness, but I feel or act them in the mind's muscles."

It is relevant to mention that, in 1895, the British writer Vernon Lee (1856–1935), pseudonym of Violet Paget, translated the German word to sympathy, explaining that there is a vivification of feelings from what we perceive which, when transformed into our own muscular efforts, allows us to fully feel, indicating *einfühlung's* relationship with muscular mimicry (Lee and Anstruther-Thomson, 1912, p. 107). Sympathy was the term commonly used to refer to empathy- related phenomena before the introduction of the term empathy into the English language as the translation of *einfühlung*, reflecting the fact that in encountering other persons, humans can resonate with and recreate that person's thoughts and emotions on different dimensions of cognitive complexity (Stueber, 2013). In this regard, Edgar Allan Poe (1809–1849), in his famous short story The Purloined Letter (Poe, 2021, p. 140), wrote:

> "When I wish to find out how wise, or how stupid, or how good, or how wicked is any one, or what are his thoughts at the moment, I fashion the expression of my face, as accurately as possible, in accordance with the expression of his, and then wait to see what

> thoughts or sentiments arise in my mind or heart, as if to match or correspond with the expression."

Poe could not have chosen a better way to penetrate the life of his characters. However, he was not the only one; the literature on emotions reveals an awareness that emotional experience takes shape through expressions of the facial muscles (Iacoboni, 2009, p. 121). For example, Nicolas Malebranche (1638–1715) already understood that "a passion in one individual will produce facial expressions and other sensible bodily effects, such as changes of color, words, cries, and the like" (1997) and, for Charles Darwin (1809–1882), "the free expression by outward signs of an emotion intensifies it; on the other hand, the repression, as far as this is possible, of all outward signs softens our emotions" (Darwin, 1872, p. 366). It is also evident that the brain can internally simulate certain emotional bodily states, as occurs in the process of transforming the emotion of sympathy into a feeling of empathy (Damasio, 2003, p. 174). In line with these observations, Titchener described becoming keenly alive to the variety of organic attitude and its kinesthetic representation (Titchener, 1909, p. 180).

The notion that feedback from emotion-specific facial reactions can causally influence other components of emotional responses, such as subjective experience and autonomic reactions, has been supported by authors such as Tomkins (Laird, 1984). Additionally, the concept of emotional facial displays serving as input to the experience of emotion has been postulated (Hess et al., 1992). The face has long been recognized as a crucial source of information for observers about a person's underlying emotional state (Hess et al., 1992). This is because the perception of a facial expression leads to unconscious emotion-specific facial mimicry and contributes to a representation in the neural production system for facial expressions (Krauthein et al., 2020).

Centuries before, Leonardo already understood that if a painter had to characterize the intentions of the mind in a narrative image, it was necessary to profoundly understand the causes that would generate such external effects; that is, to recreate the bodies and faces of the protagonists, one should follow the sensations and emotions of the dramatized situation, as he represented in The Last Supper (Kemp and Wallace, 2000, p. 70; Nadal, 2014, p. 142). In this regard, he understood that the body was the first work of the soul, its external and visible expression—modeled by the spirit of the body itself (Müntz, 2005, p. 268; Capra, 2011, p. 33).

It is interesting to note that, regarding empathy, Lipps comments that observers project themselves onto the object of their perception, that is, certain characteristics are experienced by the observer as if he or she belonged to the object, so that the object was actually felt (1924, p.1). Moreover, for Lipps, *einfühlung* means that the experience of a viewer of a gesture of pride or a joyful smile is similar to that of the individual who is experiencing the emotions related to their gestures, providing the perception of the other (1924) and is thus in agreement with Leonardo's idea that all our knowledge originates in our perceptions and feelings (Ruiz García, 2011, p. 228).

After 1,505, the expression of emotions was studied in depth by Leonardo—under the designation of "*moti mentali*" (motions of the mind)—and pointed out in several chapters of the Treatise on Painting, with the variety of faces showing the human emotional states accompanied by the attitudes of the pictorial characters and their entire body, which corresponded to the feeling expressed in their portrayed faces (Richter, 1977, p. 344). Similarly, for the romantics, art is a means to arouse emotions (Clark, 1973, p. 24) and the totality of a work of art is where all of its infinite meanings can be found — or, as Goethe defines it, it is in the plurality of a work of art that its unity is found (Benjamin, 2017, p. 150).

Although each country studied the magnificent material left to the world by Leonardo, the Romantic Movement in Germany brought an entirely new and essential idea to its study, which would become part of German artistic heritage (Adriani, 1978, p. 200). As it developed, Romanticism proposed a series of innovations with regard to human values, forming a rebellion against the static conformity of the 18th century and, in the artistic field, a rebellion against the prevailing forms imitated from Greek sculpture and the prohibition of colors and movement as expressions of life force (Clark, 1973, p. 24). Leonardo's descriptions not only reveal the deeply romantic side of his imagination, but also imply a sense of form completely at variance with that of his contemporaries, since instead of the firmly defined forms of the *quattrocento* or the enclosed forms of the High Renaissance, the subjects he describes could only be treated with the broken, suggestive forms of romantic painting (Clark, 1976, p. 81). He advised the painter to study not only marks on walls, but also the embers of the fire, or clouds, or mud, or other similar objects from which you will find most admirable ideas because, for him, from a confusion of shapes the spirit is quickened to new inventions (Clark, 1976, p. 82). It is important to note that nothing could be farther from the precepts of academic classicism than the use of stains on walls to stimulate the imagination—a procedure employed by Goya (1746–1828), one of the most anti-classical of all painters; and Victor Hugo (1802–1885), whose name is the first that comes to mind when we read Leonardo's descriptions of a deluge (Clark, 1976, p. 82).

Leonardo's greatness in the spiritual history of Germany has been inexhaustibly verified, as noted in the writings of the German Joachim von Sandrart (1606–1,688), one of the founders of art history in northern Europe, whose perspective closely resembled that of Leonardo given his view of painting as a science based on observation and his concern for organization and simplification in teaching with regard to the representation of the human body, light, and landscapes (Heck, 2009, p. 378). Sandrart's idea of the ideal painter comes from the Treatise of Leonardo and corroborates the fact that the painting of nature, performed with reason and meticulous observation, is the best method for a painter to learn their craft (Heck, 2009, p. 384). Accordingly, for Leonardo, painting is a re-creation of the visible world with the painter's imagination. It is this view of art as a creation which makes him insist that the painter must be universal, must neglect no aspect of nature and—for the same reason—he must be a scientist, that is to say, he must understand the inner nature of what he paints almost as if he had created it himself (Clark, 1976, p. 75).

For the romantics, the idea of art is the idea of its form, just as the ideal of art is the ideal of its content—pure distinctions of the philosophy of art, however, which have been little understood since the German artistic philosophy of 1800 (Benjamin, 2017, p. 152). Even Goethe did not succeed in clarifying this question—and neither did the romantics, since only a person with systematic thinking would be able to conceive the ideal of art (Benjamin, 2017, p. 152). So, naturally, an artist like da Vinci greatly appealed to the romantics (Adriani, 1978, p. 200), who aspired to infinity and loved the enigmatic, since Leonardo was rigorous and systematic, which made him react against formalisms and build his intellectual and sensory systems based on both direct observation of nature and his own criterion (Pérez de Guzmán, 2003a, p. 18).

Goethe, a fundamental contributor to German Romanticism, thought that it is measure that underlies beauty, which has its manifestation through content; however, the concept of measure is far from Romanticism, which did not accept that anything should be measured in art (Benjamin, 2017, p. 153). In this regard, it is interesting to note that for Leonardo the sense of proportion in art refers not only to numbers and measurements, but also to sounds, weights, moments, positions, humor and any other elements that may emanate the power and beauty of an image (McMurrich, 1930, p. 109; Richter, 1977, p. 228), as diverse and limitless as imagination (DeFelipe, 2014, p. 72). Like anyone who has attained a high degree of wisdom, Leonardo learned that the supreme sign of sublimity in a creation is harmony — the end toward which he aimed, as his supreme goal, in using lines and concepts, in molding the figurative expression to the spirit of the work (Biaggi, 1978, p. 447).

Goethe in particular found his own aspirations in Leonardo, with whom he had deep spiritual and artistic affinity, as noted by his admiration for the Last Supper, in particular the unusual configuration of the individuals' faces, revealing their character (Adriani, 1978, pp. 195, 200). Other well-known figures were also influenced and impressed by Leonardo's study of faces, especially due to this masterpiece which expresses intense feelings and beauty. One such figure was Albrecht Dürer (1471–1,528) —who has the most extensive and complex bibliography among German artists— in his own Gothic version of the work Christ among the Doctors (Figure 3), in which the profile of the doctor to the right of Jesus is clearly reminiscent of the work of Leonardo (Legaldano, 1972, p. 82; Clark, 1976, p. 119; Adriani, 1978, p. 200). The compositional idea of Dürer is undoubtedly Italian considering the tight group of half-figures, which resemble the style of Leonardo, but the translation is fundamentally and musically Gothic, with the fluctuating figures in the speculum almost without perspective, arranged around the four central hands — very unusual indeed in a Renaissance scheme (Legaldano, 1972, p. 115).

FIGURE 3
Albrecht Dürer: Christ among the Doctors (1506). Reproduced with permission from Museo Nacional Thyssen-Bornemisza. Copyright © Museo Nacional Thyssen-Bornemisza, Madrid. Source: https://www.museothyssen.org/en/collection/artists/durer-albrecht/jesus-among-doctors.

Among other representatives of German Romanticism, Caspar David Friedrich (1774–1840) reported that a painting must not be invented but felt; every manifestation of nature, recorded with precision, with dignity and with feeling can become the subject of art (Grummt, 2009, p. 10, 150). He also maintained that all authentic art has an inner impulse to create it, often without the artist being aware of it (Busch, 2009, p. 30). His work as a draftsman further distinguishes him within this rich, flourishing genre in Germany around 1800 (Börsh-Supan, 2009, p. 19), although, with all his singularity, he seems to approximate to the interests of Leonardo, such as in the Study of a Woman Reading and Study of a Cow and a Horse's Head (see catalog of the exhibition "Caspar David Friedrich. The Art of Drawing" Madrid: Fundación Juan March, 2009, p. 56), which includes nature, the study of a human and animals. Also for Georg Philipp Friedrich von Hardenberg, known by his pseudonym Novalis (1772–1801), the process of observation is both a subjective and objective process, an ideal and real experiment, that passes from knowledge of nature to spiritual knowledge, at which point a work of art can be contemplated (Benjamin, 2017, p. 75). Interestingly, Novalis proposed understanding empathy from *feeling* nature, as a correction to scientistic attitudes (Stueber, 2013).

These thoughts are in agreement with Leonardo since they suggest who stated that each instrument in itself must function according to the experience from which it originates and therefore advocated that when drawing a figure, one should think carefully about what it is and what one wants it to represent and, at the end, verify that this figure conforms according to the intention and the claim of its creator (Richter, 1977, pp. 239, 351). Leonardo's concern as a draftsman was to give priority to the study of gestures, attitudes and actions so that the figures could better convey the thoughts and emotions that provoked them (Pedretti, 2003, p. 95); furthermore, his conception of art as a science made him add a warning that the painter must understand the detailed structure of all that he wished to represent (Clark, 1976, p. 82).

Leonardo and the expression of art in the renaissance

> "The painter ought always to form in his mind a kind of system of reasoning or discussion within himself on any remarkable object before him. He should stop, take notes, and form some rule upon it; considering the place, the circumstances, the lights and shadows" - Invention or Composition, How a Painter ought to proceed in his studies, c. 130 (Da Vinci, 2014, p. 61).
>
> "A painter should delight in introducing great variety into his compositions, avoiding repetition, that by this fertility of invention he may attract and charm the eye of the beholder" - Invention or Composition, Of Variety in History, c. 137 (Da Vinci, 2014, p. 63).

Although it is difficult to specify precise historical dates, many Italians began to change their attitude toward the world in the late 13th century and especially in the 14th and 15th centuries (Mannering, 1981, p. 10). The most notable artists and authors of the first phase of the Renaissance movement, the so-called *quattrocento*, with spiritual freedom and free of medieval superstitions, created humanism, which allowed them to return to their reality and create their own world (Pérez de Guzmán, 2003b, p. 21), look around and rediscover nature, spiritual mystery, the harmony of ideas, and the beauty of architecture, sculptures and painting (Franqui, 2003, p. 19).

If in Greece the new culture was born among poets and philosophers, the Renaissance revolution, which emerged in Florence and then spread to other cities in Italy and Europe, had architects, sculptors and painters as protagonists, like Brunelleschi, Donatello, Massacio, Ucello, Piero della Francesca, Boticelli, Michelangelo, Rafael and Leonardo da Vinci (Franqui, 2003, p. 19). For Florentine artists, the basis of creativity and the central element for the quality of their training —and even their identity— was drawing, which was intensely admired, with well-regarded examples including the drawings of The head of Saint Anne (Figure 4) and the Battle of Anghiari, by Leonardo (Franklin, 2005, p. 18). With the Renaissance, artists felt the need to find new ways to express their thoughts and feelings and were driven to study nature and truth more deeply, since these resources could supply the artist with more effective representations than those obtained from repetitions or copies that could easily become conventional (Pedretti, 1964, p. 115; Biaggi, 1978, p. 437). The introduction of an original and vivid beauty in painting showed that the figures that once pleased artists and the public began to lose their appeal, while interest in the idea of invention or originality as an aesthetic criterion grew (Waldman, 2005, p. 32). Leonardo, whose independent mind always studied, absorbed and recreated, never copying or imitating (Steinitz, 1960, p. 116), holds a place in history against all formalism in general (Bongioanni, 1978, p. 185).

FIGURE 4
Leonardo da Vinci, The head of Saint Anne c.1510–15. Black chalk | 18.8 × 13.0 cm (sheet of paper). Public domain, via Wikimedia Commons.

When invention or originality became a condition of privilege for artists, art came to be characterized as an intellectual pursuit and not a production of work and, as a result, the status of the artist was elevated (Waldman, 2005, p. 32). The best representative of this new conception of art as an intellectual activity was Leonardo da Vinci, who defined painting as a process of investigation of the natural world, representative of his science (Kemp, 2003, p. 147; Waldman, 2005, p. 32). Leonardo describes painting as a subtle invention which —with philosophy and speculation—considers nature in all its forms (Kemp, 2003, p. 147). Indeed, his idea of imitating nature fits into the idea of invention, which is more than merely knowing, since we know by means of the intellect, but invent by means not of the intellect but of reason, and nature is not intellect, it is reason (Bongioanni, 1978, p. 185).

This new behavior exerted great influence on the visual arts and by the end of the 13th century, many artists changed the direction of their art and began to become increasingly interested in physical reality and the accurate reproduction of aspects of things, giving room to subtleties of the shape and size of objects; consequently, the study of perspective and anatomy acquired fundamental importance among artists of the Florentine Renaissance (Richter, 1977, p. 227; Mannering, 1981, p. 12). Moreover, as part of the naturalist revolution, the body was understood as a functional system between movement and emotion that included not only muscular and skeletal mechanisms, but also expressive characteristics of character and feelings, allowing the knowledge of artists and anatomists to be united, as demonstrated by Andreas Vesalius (1514–1,564) in *De Humani Corporis Fabrica*, from 1,543, which was illustrated by the artist Jan Stephan van Calcar (1499–1,546) (Kemp and Wallace, 2000, p. 13).

As a corollary of the physical body being considered as an expression of thoughts and emotions, the recognition of the potential value of figures for the demonstration of everything that can be explained through words has increased (Kemp and Wallace, 2000, p. 13). This corroborates the highest ideal of Leonardo's existence as a painter, namely the importance of painting as an instrument of knowledge (Richter, 1977, p. 101; Ramón, 2011, p. 24), a form of expression that he valued very highly due to the immediacy of its representation and potential to communicate (Vecce, 2003, p. 59). Leonardo was one of the masters who used the creation of a pictorial universe with perfection to express the truth of nature and a deep spirituality (Mannering, 1981, p. 22); for him, as a genius of acquiring knowledge from observation and experiment, the soul was the main 'sense' to appreciate more fully the infinite work of nature (McMurrich, 1930, p. 82; Tarazona, 2003, p. 52). Interestingly, other exponents of the Renaissance, such as Galileo Galilei (1564–1,642), used Leonardo's arguments to demonstrate the primacy of painting (Heck, 2009, p. 380).

Among the possibilities of expressing by illustrations, something that fascinated the artists were facial expressions, considered the most eloquent form after the hand (Kemp and Wallace, 2000, p. 97). Baroque artists such as Gian Lorenzo Bernini (1598–1,680) and Rembrandt van Rijn (1606–1,669) intensively studied faces *in extremis* to create narrative compositions with the essence of emotions, as did other artists like Charles Le Brun (1619–1,690) and Wilhelm von Kaulbach (1805–1874) (Kemp and Wallace, 2000, p. 97; Figures 5, 6). It is relevant to note that we are

FIGURE 5
Gian Lorenzo Bernini. *Anima Dannata*, 1,619 *ca.* (Roma, Palazzo di Spagna) by Sailko is licensed under CC BY 3.0. Taken from https://openverse.org/image/58719f8e-cf5a-410d-9ec1-3a47a6ce7623?q=anima%20dannata.

FIGURE 6
Head of a man with hair raised, expressing despair. Engraving – thought to be by M. Engelbrecht, 1732, after Charles Le Brun. Public Domain Mark. Source: Wellcome Collection.

observant beings and instinctively physiognomists, equipped with a visual system that perceives subtle morphological variations of the face, identifying their characteristics and the expression of emotions — from brain regions that functionally can differentiate one faces from one another and discern their specificities (Kemp and Wallace, 2000, p. 15).

Leonardo's pictorial works were eagerly awaited and brought together a variety of facial expressions reflecting human emotions attitudes and general state of the body, with expression through the limbs and particularly the hands of the subjects (as well as their posture) corresponding to the feelings expressed on their faces, such as fatigue, rest, anger, pain, fight or flight, crying, smiling, fear, command, neglect, among others (Pedretti, 1964, p. 133; Richter, 1977, p. 344). It is important to note that one of the changes introduced by Leonardo and that determined the path of Italian art of the 15th century, especially Florentine art, was an appreciation of the effects of light and shadow, the so-called *chiaroscuro* (Clark, 1976, p. 76; Mannering, 1981, p. 77). The relief, the illusion of three-dimensionality and the highlight of a flat surface together represent the essential quality of a painting and must be the first intention of a painter and this can only be achieved by capturing the play of light on the surfaces so that shadows and variations in tone suggest surface irregularities (Da Vinci, 2013, p. 154). Many of his faces and landscapes were created with imperceptible changes of tone, using a technique called *sfumato* that allowed him to achieve light plays that reflect his belief that in a painting there should be no sharply defined contours (Clark, 1976, p. 77; Mannering, 1981, p. 77). Regarding this, in Light and Shadow, Of the Beauty of Faces (c. 194), Leonardo reports (2014, p. 98):

> "You must not mark any muscles with hardness of line, but let the soft light glide upon them, and terminate imperceptibly in delightful shadows: from this will arise grace and beauty to the face."

These new techniques allowed the most reliable expression of the reality of thoughts and emotions in a pictorial universe, as Leonardo demonstrated. For example, Ginevra de Benci (1474) is portrayed with beautiful colors and enigmatic details (Figure 7); in The Adoration of the Magi (1481–1,482) and Saint Jerome (1,483, Figure 8), Leonardo captured a dramatic moment with unparalleled realism and emotional strength (Mannering, 1981, p. 25; Prat et al., 1989, p. 68); in The Last Supper (1495–1,497), which is what Dante Alighieri (1265–1,321) would have called an "alta fantasia," each character reveals a state of mind, each of which required in-depth psychological study to portray (Kemp, 2003, p. 176), with Leonardo basing his composition on the motive of a central type of innocence and beauty surrounded by embodiments of worldly passions, in this case cunning and obstinacy — such as in the Uffizi Adoration (Clark, 1976, p. 119); and Gioconda/Monalisa (1503–1,505) is a painting with the power of the human soul of Leonardo, his masterpiece revealing

FIGURE 7
Ginevra de Benci (*ca.*1474–1,478) painting in high resolution by Leonardo da Vinci. Original from The National Gallery of Art. Reproduced from rawpixel via Wikimedia Commons, licenced under CC0.

FIGURE 8
Leonardo da Vinci's Saint Jerome in the Wilderness (circa 1480). Reproduced from rawpixel via Wikimedia Commons, licenced under CC0.

his thought and work (Pater, 2013, p. 60), whose image plays with our feelings making us doubt whether or not it is a real person who actually stood in front of him (Ramón, 2011, p. 69).

Leonardo's studies to represent emotions are also related to his notes on the anatomy of the mouth, which include the investigation of the action of the muscles involved in the generation of a smile and show the extensive scientific knowledge that is behind the artistic conception of smiling figures, such as in The Virgin, the Child Jesus and Saint Anne (1503), the Mona Lisa and Saint John the Baptist (1513–1,516, Figure 9), and in screaming figures, as in the studies for the Battle of Anghiari (Figure 10) (Richter, 1977, p. 344). He studied many emotions but although he devoted himself to all the emotions related to the expressions mentioned, he does not speak of them (Pedretti, 1964, p. 133).

After his first biographer, Paolo Giovio (1483–1,552), cited Leonardo as an artist in different fields and also a scholar of optics, anatomy and music, it was Georgio Vasari (1511–1,574) who demonstrated his importance (Pérez de Guzmán, 2003a, p. 18; Heck, 2009, p. 377). However, Leonardo's work only truly became accessible to the public with the opening of the Louvre in 1800, because, until then, only the Treatise on Painting (a recompilation of his notebooks and leaves put together by Francisco Melzi (1491–1,570)) was known. This collection was kept in the Vatican Library and has been a bestseller since its first edition, in 1651 (Pérez de Guzmán, 2003a, p.17), which was followed by the London edition of 1721 and the Nuremberg edition of 1724; however, the Naples Treatise fills a very large gap as the only complete Italian language version to appear between the Paris edition and the Bologna edition of 1786 (Willette, 2009, p. 147). Overall, between 1,651 and 1898, there have been around 30 editions of the Treatise to date (Müntz, 2005, p. 205).

It is interesting to note that between the 17th century and early 19th century, Leonardo was not at the height of his influence, but over the course of the 19th century, with the emergence of Romanticism and the new spirit of transformation, he was considered a driver of modernity, fascinating diverse individuals like the French poets Theóphile Gautier (1811–1872), who in 1820 wrote in *La Presse* that Leonardo was a painter of the mysterious and compared his paintings to musical notes; Gustave Moreau (1826–1898); and Stéphane Mallarmé (1842–1898) (Pérez de Guzmán, 2003a, p. 18), as well as and Friedrich Wilhelm Nietzsche (1844–1900), who mentioned that Leonardo is one of the magical and enigmatic beings to whom supreme triumph is guaranteed (Sureda, 1998, p. 292).

Regarding modernity, it is interesting to note the syncretism that Leonardo forged between the arts, understanding them as unique and independent, but in close relationship with one another and, in this sense, he managed to change the discriminatory concept that painting maintained among the mechanical arts to integrate it into the liberal arts, thought and beauty (Franqui, 2003, p. 20). It is also important to note the strong spiritual affinity and deep admiration, mainly as a painter, that Goethe had for Leonardo and his universal genius (Adriani, 1978, p. 200; Sureda, 1998, p. 294); for instance, similar to Leonardo, he contemplates nature with analogies in the poem *Epirrhema*. The title is the name given to a part of the chorus in Greek drama, whose significance for the poem is not clear (Goethe, 1966, p. 183), although the point is that we can be 'outside' ourselves, observing our behavior, and yet know that we are still somehow inside ourselves too (Goethe, 1966, p.187). This point was eloquently expressed in the poem as follows (Mensch, 2014, p. 86):

> "You must, when contemplating nature,
>
> Attend to this, in each and every feature:

FIGURE 9
Leonardo da Vinci's Saint John the Baptist (1513–1516). Reproduced from rawpixel via Wikimedia Commons, licenced under CC0.

> There's nothing outside and nothing within,
>
> She's inside out and outside in.
>
> Thus will you grasp, with no delay,
>
> The holy secret, clear as day.
>
> […]
>
> No living thing is One, I say,
>
> But always Many."

Leonardo, empathy and the expression of his art

> "Let your figures have actions appropriated to what they are intended to think or say, and these will be well learnt by imitating the deaf, who by the motion of their hands, eyes, eyebrows, and the whole body, endeavor to express the sentiments of their mind. Do not ridicule the thought of a master without a tongue teaching you an art he does not understand; he will do it better by his expressive motions, than all the rest by their words and examples. Let then the painter, of whatever school, attend well to this maxim, and apply it to the different qualities of the figures he represents, and to the nature of the subject in which they are actors" - Expression and Character, Of Expressive Motions, c. 165 (Da Vinci, 2014, p. 85).

FIGURE 10
Leonardo da Vinci, Study of Two Warriors' Heads for the Battle of Anghiari (1775). Public domain, via Wikimedia Commons.

Leonardo was one of the most expressive personalities of the Renaissance. He was mainly an artist, but also a scientist, and knew that study, reflection and technique are preparatory, not creators of the artistic process, since the creation of art requires something more strict and directly divine, which for Leonardo was nature (Gentile, 1978, p. 163). He knew how to observe, reflect, imagine, design, draw and discover physical laws and new instruments of change (Franqui, 2003, p. 19), reacting against formalisms and building his intellectuality and senses based on his own criteria (Pérez de Guzmán, 2003a, p. 17).

He commonly reflected on nature and life on earth, with thoughts surrounded by analogies, from which appears the idea of transmigration of the spirit and the demonstration of its form of analysis and critical exposition (Cortes, 1994, p. 37). Analogical reasoning indicates that constituent parts of an organism can be compared with the other parts and that the process of idealization of a concept points to special ideas that fall into the conceptual question, that is, our analogy of physical organization is more than external (Titchener, 1909, p. 72). In this sense, Leonardo needed to visualize phenomena through their relationships (Pérez de Guzmán, 2003b, p. 23) and often states his analogies paralleling the organism of the earth with the human organism, as illustrated by the following example of his writing (Sacco, 1978, p. 457):

> "So that we might say that the earth has a spirit growth; that its flesh is the soil, its bones the arrangement and connection of the rocks of which the mountains are composed, its cartilage the tufa, and its blood the springs of water. The pool of blood which lies around the heart is the ocean, and its breathing, and the increase and decrease of the blood in the pulses, is represented in the earth

> by the flow and ebb of the sea; and the heat of the spirit of the world is the fire which pervades the earth, and the seat of the vegetative soul is in the fires, which in many parts of the earth find vent in baths and mines of sulfur, and in volcanoes" (Code Leicester, fol. 34 r).

According to the dictionary of the Royal Spanish Academy (Real Academia Española, 2022), analogy is the reasoning based on the existence of similar attributes in different beings. In fact, the sense of harmony between the different phenomena of the planet, between man and the Universe, between the micro- and the macrocosmos and the conception of the world as an immense network already existed since antiquity and remains one of the major concerns of contemporary thought (Pérez de Guzmán, 2003b, p. 23). We often end up simply depicting a character or external object rather than identifying its constitutive factors, that is, the relationship of our mind with what we see is much more than merely an exercise in pointing something out, but a necessary analysis of implication between the parts (Titchener, 1909, p. 70).

The analogies used by Leonardo meant that his drawings represented a unique scientific research method, showing that the image is not only the complementary illustration of a text, but the vehicle of a technical thought, a mental discourse (Cortes, 1994, p. 37) — the result of a developed knowledge about the truth of the things represented (Ramón, 2011, p. 69). Lipps asserts that however true it may be to say that the question of reality or non-reality does not in any way affect the essence of the work of art as an object of aesthetic contemplation, it is no less true that —not in all the arts, but in a certain class of them— a certain relationship with reality is necessary (1924, p. 59), as with Leonardo's drawings. In this regard, Titchener believed that the picture is combined with an empathic attitude and all such feelings of if, and why, and nevertheless, and therefore, normally take the form of a kind of mimicry or motor empathy (1909, p. 185). The feeling is acted out even though it may be fleeting, or it may be relatively stable; whichever it is, there is not the slightest doubt of its kinesthetic character (Titchener, 1909, p. 185).

From da Vinci's point of view, visual language had supremacy over verbal language and was key for figurative communication, especially the equivalence of mechanical arts with liberal arts, as advocated in the Treatise on Painting (Ruiz García, 2011, p. 225). Leonardo's exaltation of the importance of the eyes, which he called windows of the soul, has extraordinary anthropological value because it corresponds to the historical moment in which he lived, the transition from the medieval to the modern world, marked by the influence of visual perception on the senses of hearing and smell in the representation of the human being and its relationship with the natural world (Vecce, 2003, p. 61). Other well-known figures in the 20th century were supportive of this view, including Virginia Woolf (1882–1941), who wrote in *Books and Portraits* (Woolf, 1977, p. 36):

> "The heather is not much, and the rock is not much; but the heather and the rock, discerned in their living expressional relationship by the poetic eye, are very much indeed — a beauty which is living with the life of man, and therefore inexhaustible … but true poets and artists know that this power of visual synthesis can only be exercised, in the present state of our faculties, in a very limited way; hence, there is generally, in the landscapes and descriptions of real genius, a great simplicity in and apparent jealousy of their subjects, strikingly in contrast with the works of those who fancy that they are describing when they are only cataloging."

For Leonardo, painting had the necessary signals to express different languages and, although he recognizes the presence of writing, he considers it as a form of drawing when commenting that writers draw with the pen what is found in their mind (Vecce, 2003, p. 61). There is no better way to verify this fact than to contemplate his signature, which denotes a great vital dynamism, an imaginative mind, a taste for originality and an enviable aesthetic sense (Ruiz García, 2011, p. 199; see Leonardo's notes in Figure 11).

The relationship between image and word is one of the fundamental elements in Leonardo's work through which he plays with drawings and writings with genius and innovation, freely and without the correct construction of language, metric or cultural traditions (Pérez de Guzmán, 2003b, p. 28; see Leonardo's pictographs in Figure 12). Leonardo believed that to produce a result by means of an instrument to drawn or write does not allow does not allow yourself to complicate it by introducing many subsidiary parts, but rather results in following the briefest way possible, without acting as those who do not know how to express a thing in its own proper vocabulary and proceed by a method with great prolixity and confusion (Richter, 1977, p. 245).

The point of Leonardo's drawings was to make an object immediately visible, with little explanation required, that is, to highlight the relationship between who sends the message and who receives it — an approach that marked the beginning of modern science, and one that Leonardo employed to convey the meaning of his games between figures and words (Vecce, 2003, p. 69). As a matter of fact, mental constitution is widely varied, and the meaning response of a mind of a certain constitution varies widely under varying circumstances; all conscious meaning is carried either by total kinesthetic attitude or by words — as well as by all sorts of sensational and imaginal processes (Titchener, 1909, p. 178).

Leonardo's drawings show his speculative thinking — and imagination was undoubtedly utmost in his mind, as he used iconic elements as substitutes for corresponding words, in line with the notion of the predominance of figurative resource over

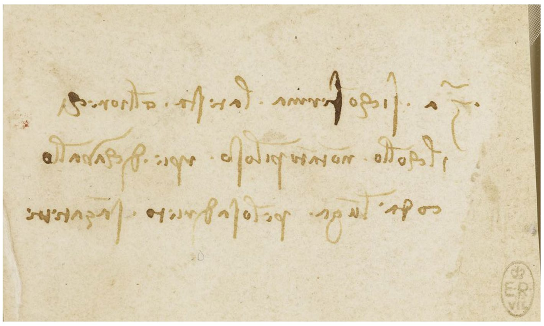


FIGURE 11
Notes on the appearance of horses c.1490. Some written notes in Leonardo's hand. Pen and ink | 5.0 × 8.1 cm (sheet of paper). Public domain, via Wikimedia Commons.

FIGURE 12
Leonardo da Vinci, Pictographs c.1487–90. A scrap of puzzle-writing, the first line being made of musical notes to be interpreted on the la, sol, mi, fa system. In the middle, the beginning of various attempts to put into pictographs the sentence previously given. Pen and ink | 6.0 × 10.3 cm (sheet of paper). Public domain, via Wikimedia Commons.

FIGURE 13
Leonardo da Vinci, A rearing horse, and heads of horses, a lion and a man. c.1503–4. Pen and ink, wash, a little red chalk. | 19.6 × 30.8 cm (sheet of paper). Public domain, via Wikimedia Commons.

FIGURE 14
Leonardo da Vinci, The bust of a man, and the head of a lion c. 1,510. Red chalk, touches of white chalk, on orange-red prepared paper | 18.3 × 13.6 cm (sheet of paper) Public domain, via Wikimedia Commons.

linguistic resource (Ruiz García, 2011, p. 216). The angel prototype that Leonardo painted in Baptism of Christ and the teenager in Adoration of the Magi are examples in which his imaginative soul guided his hands in forming an image with its own characteristics (Steinitz, 1960, p. 118). Thus, one of the elements of Leonardo's research, in addition to his artistic ability, and search for scientific knowledge, was fantasy or creative imagination, always linked to the intellectual understanding of nature (Capra, 2011, p. 63). He was clearly convinced that fantasy was an imaginative extension of rational thought rather than a negation of it (Kemp, 2003, p. 147). Eugène Müntz, a French art historian (1845–1902), declared that no artist was so independent as to interpret both imagination and creation (Steinitz, 1960, p. 118).

Leonardo's drawings and writings are the result of rigorous and systematic observation accompanied by isolated moments of disorganized expression; in other words, they are eminently mental constructions in which calculated synthesis captures the sensitive information of what is observed to shape and organize his work (Bongioanni, 1978, p. 184). Over the centuries, efforts have been made to explain and codify the outward manifestations of character, thoughts, and emotions, which Leonardo called *il concetto dell'anima* - the intention of the mind (Kemp and Wallace, 2000, p. 16). In this sense, he believed that the most important thing in painting the human figure was to represent mental states and emotions, since the expression of the human spirit through art was the artist's greatest aspiration (Capra, 2011, p. 33). Moreover, a true painter should know the truth of the things he represents to make it possible to see the nature of what is expressed by art (Ramón, 2011. p. 26). For Leonardo, discovering nature meant finding an order of connection that the discoverer is a part of and in which he identifies the sense of his presence in the idealized system (Bongioanni, 1978, p. 184).

Leonardo recognized that for the painter to understand the structure of a figure in order to give expression to his spirit, it was fundamental to study —in different species, ages and sexes (Figures 13, 14)— the different body constitutions; anatomy; relations and proportions; attitudes; movements; and mimetic elements (Biaggi, 1978, p. 439). In this way, it is possible to communicate feelings, impressions and ideas and reproduce reality with the greatest accuracy (Pedretti, 2003, p. 94). For him, the painter ought to study methodically and leave nothing unmemorized and he must observe how limbs and joints vary from one animal to another (Richter, 1977, p. 101).

The various aesthetic images, as possible alternatives of logical meaning, often share their functions with the sensations of movement (Titchener, 1909, p. 21). Thus, whenever one feels oneself from the observation of an attitude or gesture in an external object, this projection of the object itself is the very

FIGURE 15
Leonardo da Vinci, Portrait of a young woman in profile c.1490 (RCIN 912505). Public domain, via Wikimedia Commons.

feeling triggered by an inner effort (Lipps, 1924, p. 7). At a basic level, *einfühlung* points to feeling of belonging in the world; likewise, it refers to an immediate and intersubjective relational experience —a kinetic inner imitation— a mirroring of the expression observed that carries affectively perceived sensorimotor impressions (Stamatopoulou, 2018, p. 170). In this sense, Leonardo possessed that rare combination of vitality, strength and delicacy which only a few of the greatest draftsmen have achieved (Kemp, 2003, p. 33; also see Figure 15) and that provides the observer with a voluntary and conscious activity of fantasy and contemplation of objects. Furthermore, the richness of the artist's fantasy is, therefore, the richness of that which happens in the work, or richness of its content, concretely, of moments of inner vitality expressed in the work (Lipps, 1924, p. 95). In Expression and Character, from Of the Variety of Faces (c. 170), Leonardo states (2014, p. 86):

> "The countenances of your figures should be expressive of their different situations: men at work, at rest, weeping, laughing, crying out, in fear, or joy, and the like. The attitudes also, and all the members, ought to correspond with the sentiment expressed in the faces."

Leonardo and Vesalius were the pioneers in demonstrating what was possible with anatomical illustrations, from which artists developed aspirations to encourage the viewer to become a witness of what he saw (Kemp and Wallace, 2000, p. 33). In this regard, he affirmed that the painted figures should be created so that the observer could easily know, through the movements and attitude of the figures, the mental situation of the creator of the narrative and the meaning of his intentions (Da Vinci, 2013, p. 121, c. 294), since an experiencer must empathize with an observer in order to think, understand and communicate as he does (Titchener, 1909, p. 185). After all, there is no doubt that the expression of emotions and feelings are an integral part of who we are, personally and socially (Damasio, 2003, p. 247).

Leonardo's painting is not understood at first sight; a mental process is required on the part of the observer to reconstruct and appreciate all its richness of expression, movement, gesture and aesthetic configuration. The spectator must create unity, just as the ear perceives a series of notes and silences that the listener's brain configures as something invisible (Pérez de Guzmán, 2003c, p. 117). As with other brain functions, it seems that we have to learn to appreciate art, sometimes by a cultural or a perceptual transformation (DeFelipe, 2014, p. 78). The harmony of his work is not born directly from the figure, but from an infinity of details that, together, constitute the work. As Leonardo put it, details make perfection, and perfection is not a detail (Pita, 2019, p. 39).

Finally, thanks to the development of social neuroscience, which combines classical cognitive neuroscience and social psychology, using multi-level and multidisciplinary approaches, the neural basis of empathy is being unraveled (e.g., see Bernhardt and Singer, 2012). Furthermore, greater links between neuroscience and the humanity field can be seen represented by enhanced communication encompassing neuroscience and the humanities, clear conceptual overlap between both fields, and new actionable outcomes (Carew and Ramaswami, 2020). Who could have imagined that Leonardo's dream of explaining artistic perception with a mechanistic model would become a feasible scientific goal as it is presently?

Author contributions

SM: Investigation, Writing – original draft, Conceptualization, Writing – review & editing. JD: Supervision, Writing – review & editing, Funding acquisition.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was supported by the following grants: PID2021-127924NB-I00 (to JD) funded by MCIN/AEI/10.13039/501100011033.

Acknowledgments

We would like to thank Nick Guthrie for his excellent editorial assistance.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Adriani, G. (1978). "Leonardo in Germany" in *Leonardo da Vinci*. ed. K. Clark (New York, NY: Reynal and Company), 195–200.

Barker, L.F. (1899). *The nervous system and its constituent neurones*. New York: D. Appleton and Company.

Baron-Cohen, S., and Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *J. Autism Develop. Disord.* 34, 163–175. doi: 10.1023/b:jadd.0000022607.19833.00

Benjamin, W. (2017). *El Concepto de Crítica de Arte en el Romanticismo Alemán*. Madrid: Abada Editores.

Bernhardt, B., and Singer, T. (2012). The neural basis of empathy. *Annu. Rev. Neurosci.* 35, 1–23. doi: 10.1146/annurev-neuro-062111-150536

Biaggi, C. F. (1978). "Anatomy in art," in *Leonardo Da Vinci*. ed. K. Clark (New York, NY: Reynal and Company), 437–447.

Bongioanni, F. M. (1978). "Studying Leonardo" in *Leonardo da Vinci*. ed. K. Clark (New York, NY: Reynal and Company), 175–186.

Börsh-Supan, H. (2009). "Changes in Friedrich's Drawings" in *Caspar David Friedrich. The art of drawing*. ed. F. J. March (Madrid: Fundación Juan March), 11–19.

Braadbaart, L., Grauw, H., Perrett, D., Waiter, G., and Williams, J. (2014). The shared neural basis of empathy and facial imitation accuracy. *NeuroImage* 84, 367–375. doi: 10.1016/j.neuroimage.2013.08.061

Busch, W. (2009). "Notations of Friedrich's drawings" in *Caspar David Friedrich. The art of drawing*. ed. F. J. March (Madrid: Fundación Juan March), 21–29.

Capra, F. (2011). *La Ciencia de Leonardo. La naturaleza profunda de la mente del gran genio del Renacimiento*. Barcelona: Editorial Anagrama.

Carew, T., and Ramaswami, M. (2020). The neurohumanities: an emerging partnership for exploring the human experience. *Neuron* 108, 590–593. doi: 10.1016/j.neuron.2020.10.019

Clark, K. (1973). *La Rebelión Romántica. El arte romántico frente al clásico*. Madrid: Alianza Editorial.

Clark, K. (1976). *Leonardo da Vinci. An account of his development as an artist*. Londres: Penguin Books.

Cortes, V. (1994). *Anatomia, Academia y Dibujo Clásico*. Madrid: Cátedra.

Da Vinci, L. (2013). *Leonardo da Vinci. Tratado de la Pintura*. Buenos Aires: Losada.

Da Vinci, L. (2014). *A treatise on painting, by Leonardo da Vinci*. London: Maxtor.

Damasio, A. (2003). *En busca de Spinoza: neurobiología de la emoción y los sentimientos*. Barcelona: Crítica.

Darwin, C. (1872). *The expression of the emotions in man and animals*. London: Albemarle

Decety, J. (2011). Dissection the neural mechanisms mediating empathy. *Emot. Rev.* 3:1. doi: 10.1177/175407391037466

DeFelipe, J. (2014). *El Jardín de la Neurología. Sobre lo bello, el arte y el cerebro*. Madrid: Consejo Superior de Investigaciones Cientificas y Boletín Oficial del Estado.

DeFelipe, J. (2017). *Cajal's neuronal Forest*. New York: Oxford University Press.

Franklin, D. (2005). "Revealing magnificence and grandeur Florentine drawing in the first half of the sixteenth century" in *Leonardo da Vinci, Michelangelo, and the renaissance in Florence*. ed. D. Franklin (Ottawa, CA: National Gallery of Canada in association with Yale University Press), 18–29.

Franqui, C. (2003). "La Ciudad de Leonardo" in *Leonardo da Vinci y la Música*. Madrid: Ministerio de Cultura, Biblioteca Nacional, 12–20.

Freedberg, D., and Gallese, V. (2017). Motion, emotion and empathy in esthetic experience. *Trends Cogn. Sci.* 11, 197–203. doi: 10.1016/j.tics.2007.02.003

Gentile, G. (1978). "The thought of Leonardo" in *Leonardo da Vinci*. ed. K. Clark (New York, NY: Reynal and Company), 163–174.

Goethe, J. W. (1966). *Poems of Goethe*. Cambridge: Cambridge University Press.

Grummt, C. (2009). "Two sketchbook pages: new discoveries in Friedrich scholarships" in *Caspar David Friedrich. The art of drawing*. ed. F. J. March (Madrid: Fundación Juan March), 151–157.

Heck, M.-C. (2009). "The reception of Leonardo da Vinci's Trattato della Pittura, or Traitté de la Peinture, in seventeenth-century northern Europe" in *Re-Reading Leonardo. The treatise on painting across Europe, 1550–1900*. ed. C. Farage (Surrey, R.U: Ashgate Publishing Limited), 377–414.

Hess, U., Kappas, A., McHugo, G., Lanzetta, J., and Kleck, R. (1992). The facilitative effect of facial expression on the self-generation of emotion. *Int. J. Psychophysiol.* 12, 251–265.

Iacoboni, M. (2009). *Las neuronas espejo: empatía, neuropolítica, autismo, imitación o de cómo entendemos a los otros*. Madrid: Katz

Kemp, M. (2003). Drawing the boundaires, in VinciLeonardo da and Master Draftsman, ed. The Metropolitam Museum of Art New York, NY: *The Metropolitam Museum of art*, 141–154.

Kemp, M., and Wallace, M. (2000). *Spectacular bodies. The art and science of the human body from Leonardo to now*. London: Hayward Gallery.

Krauthein, J., Steines, M., Dannlowski, U., Neziroglu, G., Acosta, H., Sommer, J., et al. (2020). Emotion specific neural activation for the production and perception of facial expressions. *Cortex* 127, 17–28. doi: 10.1016/j.cortex.2020.01.026

Laird, J. (1984). The real role of facial response in the experience of emotion: a reply to Tourangeau and Ellsworth, and other. *J. Pers. Soc. Psychol.* 47, 909–917. doi: 10.1037/0022-3514.47.4.909

Landrus, M. (2006). *Los Tesoros de Leonardo da Vinci*. Barcelona: Librería Universitaria de Barcelona.

Lee, V., and Anstruther-Thomson, C. (1912). *Beauty and ugliness: and other studies in psychological aesthetics*. London: John Lane.

Legaldano, P. (1972). *La Obra Pictórica Completa de Durero*. Barcelona and Madrid: Editorial Noguer.

Lipps, T. (1924). *Los Fundamentos de la Estética*. Madrid: Luiz Faure.

Mannering, D. (1981). *El Arte de Leonardo da Vinci*. Barcelona: Ediciones Polígrafa.

McMurrich, J. P. (1930). *Leonardo da Vinci. The Anatomist*. Baltimore: The Williams & Wilkins Company.

Mensch, J. (2014). The poem as plant: Archetype and metamorphosis in Goethe and Schlegel. Available at: https://philpapers.org/archive/MENTPA-7.pdf (Accessed June 19, 2023).

Muncer, S., and Ling, J. (2006). Psychometric analysis of the empathy quotient (EQ) scale. *Pers. Individual Diff.* 40, 1111–1119. doi: 10.1016/j.paid.2005.09.020

Müntz, E. (2005). *Leonardo da Vinci. El sabio, el artista, el pensador*. Barcelona: Liberduplex.

Nadal, C. J. (2014). "Leonardo da Vinci" in *El Hombre, la Naturaleza, la Mirada* (Madrid: Ediciones del Oriente y del Mediterrâneo).

Pater, W. (2013). "La Gioconda" in *Leonardo da Vinci. Tratado de la Pintura* ed. Losada. (Buenos Aires, BA: Losada), 60–61.

Peacocke, A. (2023). Aesthetic experience. Available at: https://plato.stanford.edu/entries/aesthetic-experience/ (Accessed January 25, 2023).

Pedretti, C. (1964). *Leonardo da Vinci on painting. A lost book (Libro a). Reassembled from the codex Vaticanus Urbinas 1270 and from the codex Leicester with a chronology of Leonardo's "treatise on painting"*. Berkeley and Los Angeles: University of California Press.

Pedretti, C. (2003). "The critical fortune of Leonardo's drawings," in *Leonardo da Vinci: Master Draftsman*. ed. C. C. Bambach. The Metropolitam Museum of Art New York, NY: *The Metropolitam Museum of art*, 79–110.

Pérez de Guzmán, M. (2003a). "Abarcando a Leonardo" in *Leonardo da Vinci y la Música*. Madrid: Ministerio de Cultura, Biblioteca Nacional, 15–18.

Pérez de Guzmán, M. (2003b). "Pensamiento" in *Leonardo da Vinci y la Música*. Madrid: Ministerio de Cultura, Biblioteca Nacional, 21–32.

Pérez de Guzmán, M. (2003c). “La música y la armonía en la pintura de Leonardo” in *Leonardo da Vinci y la Música*. Madrid: Ministerio de Cultura, Biblioteca Nacional, 115–124.

Pevsner, J. (2002). Leonardo da Vinci's contributions to neuroscience. *Trends Neurosci.* 25, 217–220. doi: 10.1016/s0166-2236(00)02121-4

Pita, J. R. (2019). *Leonardo da Vinci. Pensamientos*. Madrid: Verbum.

Poe, E. A. (2021). *The essential Tales and Poems of Edgar Allan Poe*. New York: Chartwell Books.

Prat, J., Molina, C., Solé, R., and Dorico, C. (1989). *Maestros de la Pintura. La Obra Completa de Leonardo*. Barcelona: Origen.

Preston, S., and De Waal, F. B. M. (2002). Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–20. doi: 10.1017/S0140525X02000018

Ramón, S. P. (2011). *La Pintura Religiosa de Leonardo da Vinci. Su Legado Humanista y Cristiano*. Barcelona: Erasmus Ediciones.

Real Academia Española. (2022). Diccionario de la Lengua Española. Available at: https://dle.rae.es/analog%C3%ADa (Accessed November 5, 2022).

Richter, J. P. (1977). *The literary works of Leonardo da Vinci*. Edinburgh: R. & R. Clark Limited.

Ruiz García, E. (2011). *Claves de una Mente Prodigiosa. Leonardo da Vinci*. Madrid: Canal de Isabel II.

Sacco, F. (1978). Da Vinci's geology and geography, in *Leonardo da Vinci*. ed. K. Clark (New York, NY: Reynal and Company), 455–466.

Singer, T., and Klimecki, O. (2014). Empathy and compassion. *Curr. Biol.* 24, R875–R878. doi: 10.1016/j.cub.2014.06.054

Stamatopoulou, D. (2018). Empathy and the aesthetic: why does art still move us? *Cogn. Process.* 19, 169–186. doi: 10.1007/s10339-017-0836-3

Steinitz, K. T. (1960). *Leonardo da Vinci's concept of the antique*. Aohnai, ATH: IV Congrès International D'Esthétique.

Stueber, K. (2013). Empathy. Available at: https://plato.stanford.edu/entries/empathy/ (Accessed October 20, 2022).

Sureda, J. (1998). *Summa Pictorica IV. El Renacimiento Italiano*. Spain: Planeta.

Tarazona, A. R. (2003). “La Música en la Época de Leonardo da Vinci (1452-1519)” in *Leonardo da Vinci y la Música, ed. Biblioteca Nacional de España y Auditorio de Tenerife* (Madrid), 43–64.

Titchener, E. B. (1909). *Experimental psychology of the thought-process*. New York: The Macmillan Company.

Vecce, C. (2003). “Word and image in Leonardo's writing”, in *Leonardo da Vinci: Master Draftsman*. ed. C. C. Bambach The Metropolitam Museum of Art New York, NY: *The Metropolitam Museum of art*, 59–78.

Vischer, R. (1873). “On the optical sense of form: a contribution to aesthetics” in *Empathy, form, and space*. eds. H. F. Mallgrave and E. Ikonomou (Santa Monica, CA: The Getty Center for the History of Art and the Humanities), 89–123.

Waldman, L. A. (2005). “Ingenious and subtle spirits Florentine painting in the first half of the sixteenth century” in *Leonardo da Vinci, Michelangelo, and the renaissance in Florence*. ed. D. Franklin (Ottawa, CA: National Gallery of Canada in association with Yale University Press), 30–43.

Willette, T. (2009). “The first Italian publication of the treatise on painting: book culture, the history of art, and the Naples edition of 1733” in *Re-Reading Leonardo. The treatise on painting across Europe, 1550–1900*. ed. C. Farage (Surrey, R.U: Ashgate Publishing Limited), 147–171.

Woolf, V. (1977). *Books and portraits*. New York: Harcourt Brace Jovanovich.

Zölzer, F., and Zölzer, N. (2020). Empathy as an ethical principle for environmental health. *Sci. Total Environ.* 705:135922. doi: 10.1016/j.scitotenv.2019.135922

Frontiers in Psychology

TYPE Mini Review
PUBLISHED 10 April 2024
DOI 10.3389/fpsyg.2024.1269820

OPEN ACCESS

EDITED BY
Florin Dolcos,
University of Illinois at Urbana-Champaign,
United States

REVIEWED BY
Gunter Kreutz,
University of Oldenburg, Germany
Marco Antonio Correa Varella,
Federal University of Pernambuco, Brazil

*CORRESPONDENCE
Manuela M. Marin
✉ a09811757@unet.univie.ac.at;
✉ manuela.marin@fh-krems.ac.at

RECEIVED 30 July 2023
ACCEPTED 29 March 2024
PUBLISHED 10 April 2024

CITATION
Marin MM and Gingras B (2024) How music-induced emotions affect sexual attraction: evolutionary implications.
Front. Psychol. 15:1269820.
doi: 10.3389/fpsyg.2024.1269820

How music-induced emotions affect sexual attraction: evolutionary implications

Manuela M. Marin[1,2]* and Bruno Gingras[2,3]

[1]Department of Cognition, Emotion and Methods in Psychology, University of Vienna, Vienna, Austria, [2]Austrian Research Institute of Empirical Aesthetics, Innsbruck, Austria, [3]Department of Cognitive Biology, Faculty of Life Sciences, University of Vienna, Vienna, Austria

More than a century ago, Darwin proposed a putative role for music in sexual attraction (i.e., sex appeal), a hypothesis that has recently gained traction in the field of music psychology. In his writings, Darwin particularly emphasized the charming aspects of music. Across a broad range of cultures, music has a profound impact on humans' feelings, thoughts and behavior. Human mate choice is determined by the interplay of several factors. A number of studies have shown that music and musicality (i.e., the ability to produce and enjoy music) exert a positive influence on the evaluation of potential sexual partners. Here, we critically review the latest empirical literature on how and why music and musicality affect sexual attraction by considering the role of music-induced emotion and arousal in listeners as well as other socio-biological mechanisms. Following a short overview of current theories about the origins of musicality, we present studies that examine the impact of music and musicality on sexual attraction in different social settings. We differentiate between emotion-based influences related to the subjective experience of music as sound and effects associated with perceived musical ability or creativity in a potential partner. By integrating studies using various behavioral methods, we link current research strands that investigate how music influences sexual attraction and suggest promising avenues for future research.

KEYWORDS

origins of music, mate choice, sex appeal, sexual selection, arousal transfer, social bonding, evolution of musicality, dating

1 Introduction

Music, besides language, is one of the main distinctive characteristics of the human species (Benítez-Burraco and Nikolsky, 2023). Whereas language is primarily a means to communicate semantic meaning, music is a powerful elicitor of emotions (e.g., Juslin and Sloboda, 2011; Marin and Bhattacharya, 2011). Music fulfills a myriad of functions in our daily lives (Clayton, 2016) that go beyond pure entertainment and music-induced pleasure (Pinker, 1997). Abundant empirical evidence for a socio-biological basis of music has accumulated over the recent years, which suggests that music may have evolved through sexual and/or natural selection (Huron, 2001; Wallin et al., 2001; Honing and Ploeger, 2012), though the exact selection mechanism has been a longstanding topic of debate (Kleinman, 2015). In this review, we present evidence suggesting that music may have evolved through sexual selection as proposed by Darwin (1871). In our discussion on the putative role of music in mate choice, particular emphasis will be placed on underlying psychological mechanisms based on music-induced emotions in listeners.

2 Origins of musicality

One difficulty encountered when studying the origins of music is that, although music is a phenomenon observable in most, if not all, cultures (Blacking, 1973), it turns out to be difficult to define according to universally observable characteristics such as rhythm or pitch (Savage et al., 2015). Some musical genres have no underlying isochronous pulse (e.g., Tibetan monotone chanting, Bispham, 2009), whereas others do not make use of discrete pitches (e.g., some compositions by Xenakis). Thus, from an evolutionary perspective, it may prove more useful to study the origins of *musicality*, defined as the set of traits associated with the capacity to produce and enjoy *music*, defined as the cultural end-product of musicality (Honing et al., 2015).

Another difficulty is that musical practice leaves only few artifacts such as recordings or fossilized vocal organs (Killin, 2018). Consequently, accounts of the origins of music remain in large part interpretative: scientists attempt to reconstitute the past based on scant pre-historical evidence, such as bone flutes that are at least 35,000 years old in *Homo Sapiens* (Conard et al., 2009) and Neanderthals (Turk et al., 2020), but musical behavior such as singing, drumming and dancing cannot be traced back to fossils. One could tentatively speculate, based on the existence of these bone flutes, that the common ancestor of both species was to some extent already musical 631-789 k years ago (Beerli and Edwards, 2002). However, both species were interbreeding for a while in Europe (Nigst et al., 2014; Vidal-Cordasco et al., 2023), which weakens such speculations. The current archeological evidence is augmented by complementary comparative evidence such as cross-cultural studies, which look for common features or universals (Brown and Jordania, 2013), or cross-species comparisons, which are used to draw inferences about ancestral forms and putative adaptive functions associated with musicality.

Among the current accounts of the origins of music, a broad dichotomy can first be observed between adaptationist and non-adaptationist theories. Whereas the former propose that musicality, as a trait, plays a role in the survival of the human species, the latter consider music to be either a "technology" or a byproduct of other adaptations which plays no evolutionary role (Pinker, 1997). Adaptationist accounts can be further subdivided according to the principal function they ascribe to musicality, or to the mode of selection (natural versus sexual). Sexual selection itself comprises two pathways, namely intrasexual competition, involving dominance and prestige (Fisher and Candea, 2012; Varella et al., 2017), and intersexual selection, associated with fitness indicators as well as aesthetic aspects (see Prum, 2012; Davis and Arnocky, 2022). Modern sexual selection theory discusses several intersexual processes, such as good taste (Davis and Arnocky, 2022), good genes, good partners, and good providers (Buss and Shackelford, 2008), good parents (Kreutz and Feldhaus, 2023) and good relationship maintenance (Evans et al., 2022). Crucially, adaptationist accounts are not necessarily mutually exclusive: although various theories emphasize distinct, and possibly complementary, functions for musicality, they broadly agree that evolutionary pressures played a defining role in the origins of musicality.

In aesthetics, one frequently discussed account is Darwin's sexual selection hypothesis (Darwin, 1871; Prum, 2012; Renoult, 2016; Kalinowski et al., 2021), according to which music acts as a courtship display in reproductive mate choice. Darwin's hypothesis, which states that trait-preference covariation may occur without necessarily having a biological function, was revived by Miller (1999, 2000, 2001), who emphasizes the fitness indicator role of the sexually selected trait (see also Sluming and Manning, 2000) and regards music as an honest signal. Supporting this hypothesis, Miller noticed that interest for music peaks in adolescence and that young male musicians produce more music than female musicians (see also Savage et al., 2015). Musicality was also reported to be a preferred trait in romantic partners (Kaufman et al., 2016).

Another longstanding theory is based on the idea that music and language have a common origin (Darwin, 1871), with language subsequently specializing in the communication of semantic meaning, and music primarily conveying emotions (Ma et al., 2019). This account, recently revisited by researchers such as Brown (2000a) and Mithen (1998), has been strengthened by neuroimaging evidence showing that music and language processing share neural resources (Koelsch et al., 2004; Patel, 2008). Language itself may be a product of sexual selection (Worden, 2022), and since both communication systems may have co-evolved (Benítez-Burraco and Nikolsky, 2023), positive effects of music on sexual attraction are probably not a recent phenomenon. Other theories suggest a role for music in promoting group cohesion (Dunbar, 2004; Savage et al., 2021), mood-regulation (Sloboda and O'Neill, 2001), mother-infant bonding (Trehub, 2003; Dissanayake, 2008; Mehr et al., 2021), territorial defense (Hagen and Hammerstein, 2009), or cognitive and social development (Cross, 2001). Future studies should aim to show which aspects of musicality can solidly be ascribed to either natural or sexual selection and which ones cannot. In this process, as long as they are all grounded in natural selection, distinct theories may be easier to subsume under an overarching theory (Savage et al., 2021), but as soon as sexual and natural selection mechanisms both play a role, theory building becomes more challenging (Keller et al., 2023). Another related challenge will be to develop explanatory theories that describe the specific evolutionary mechanisms involved in the emergence of musicality, along with their respective time-scales (see also Novaes and Natividade, 2023).

To be logically consistent with evolutionary theory, adaptive accounts require evidence of the heritability of at least some components of musicality, as well as evidence of the presence of a selectively acquired function (Justus and Hutsler, 2005; McDermott and Hauser, 2005; Croston et al., 2015). While it is difficult to assess the selective pressures faced by our ancestors with respect to musicality (Honing et al., 2015), studies have shown a large phenotypic variability in musicality among humans (Müllensiefen et al., 2014), which is at least partly heritable (Gingras et al., 2015a; Mosing et al., 2015; Wesseldijk et al., 2023). Thus, currently available evidence suggests that adaptationist accounts of the origins of musicality have cleared this initial hurdle, although much work remains to be done.

With respect to Darwin's sexual selection hypothesis, Mosing et al. (2015) reported that, although some components of musicality, such as pitch, melody, and rhythm perception (as measured by test batteries, see Ullén et al., 2014), were moderately heritable in a sample of over 10,000 Swedish twins, musical ability and mating success were negatively associated. Moreover, Harrison and Hughes (2017) reported similar sexual activity for musicians and non-musicians (but see Lange and Euler, 2014). However, recent experimental studies have provided support for Darwin's hypothesis (see Section 4).

3 Music-induced emotions

The study of emotions expressed or induced by music has a long history (e.g., Juslin and Sloboda, 2011). Music has repeatedly been shown to induce the expressive, psychophysiological and subjective feeling components of an emotion episode (Krumhansl, 1997; Ogg et al., 2017; Fuentes-Sanchez et al., 2021), as proposed by Scherer (2009) in his component process model of emotion. Indeed, music can induce intense pleasure and chills (Blood and Zatorre, 2001; Grewe et al., 2007) and emotional lacrimation (Wassiliwizky et al., 2017; Mori and Iwanaga, 2021). These strong pleasurable responses are mostly due to music's ability to activate the human reward system (Ferreri et al., 2019; Fasano et al., 2023) and to induce emotional arousal responses in listeners (Schafer and Sedlmeier, 2011; Gingras et al., 2015b). Arousal has also been found to be a correlate of perceived musical complexity, which is central to Berlyne's psychobiological model of aesthetic responses (Berlyne, 1960; Marin, 2022). Another key finding is that similar acoustical cues convey emotion communication in speech and music (Juslin and Laukka, 2003), which supports the hypothesis of a common origin of music and speech (see Section 2).

The psychological mechanisms through which music induces emotions are manifold and involve various brain functions. They can be described as brain stem reflex, rhythmic entrainment, emotional contagion, musical expectancy, evaluative conditioning, visual imagery, episodic memory and aesthetic judgment (Juslin, 2013). Each mechanism is hypothesized to have a specific adaptive value and to be associated with specific types of affective responses. Music has been documented to induce emotions and moods in various social and situational contexts, ranging from live music concerts to self-selected music listening in private and public spaces (Sloboda and O'Neill, 2001; Juslin and Laukka, 2004; North and Hargreaves, 2008). In these various contexts, music can consciously or unconsciously influence people's feelings and behavior (North and Hargreaves, 2008). For example, background music can affect eating behavior as well as time and money spent in restaurants (Stroebele and de Castro, 2006; Beer and Greitemeyer, 2019). Film music is a prominent example of how the processing of visual information can be altered by musical emotions (Steffens, 2020; Herget, 2021), and musical arousal even impacts driving behavior (van der Zwaag et al., 2013; Navarro et al., 2019). Music listening is also an excellent means of regulating one's emotions in a wide range of everyday situations outside the therapeutic context (Cook et al., 2019; Bachman et al., 2022; Garrido et al., 2022). Positive effects of emotion regulation by music have also been reported in the context of child care, parent-infant communication and social bonding (Persico et al., 2017; Cirelli et al., 2020; Whittall et al., 2023).

4 Musicality and its role in sexual attraction

Following Miller's (2001) revival of Darwin's sexual selection hypothesis, Charlton et al. (2012) and Charlton (2014) experimentally tested the idea that females may be more sensitive to musical cues signalling genetic quality during peak fertility (Gangestad and Thornhill, 2008). The 2012 study used simple computer-generated melodies that varied in complexity. One group of females rated the complexity of the musical stimuli, whereas a second group gave liking ratings for the same stimuli at two points during the menstrual cycle (fertile versus infertile). The results did not reveal a significant effect of conception risk on liking ratings. In Charlton's (2014) follow-up study, one group of female participants listened to pairs of laboratory-generated musical excerpts, allegedly from different composers, and was asked to choose which composer sounded the most complex. A second group was asked to indicate which composer they preferred as a sexual partner in either a short-term or a committed long-term relationship. Conception risk affected preference ratings for a short-term relationship, with females in the fertile phase of their cycle preferring composers of complex melodies, but not for a long-term one. These findings suggest that musical creativity could be an indicator of "good genes" and were interpreted as evidence for sexual selection (see also Miller, 2001; Haselton and Miller, 2006; Varella et al., 2022).

Although Charlton's studies did not test males, they introduced elegant experimental paradigms demonstrating that musical creativity and complexity may influence female mate choice. However, because complexity is associated with higher arousal (see Section 3), it is unclear whether participants based their decisions purely on the quality of the musical compositions and their complexity (as an indicator of creativity) or whether the reported effects may be explained by arousal induction. Moreover, Charlton focused on the effects of musical sound in isolation, without accounting for other potential mating cues.

To circumvent these limitations, Marin et al. (2017) and Marin and Rathgeber (2022) developed a crossmodal priming paradigm to examine whether music and musicality affect sexual attraction in females and males. This research strand builds upon a body of studies suggesting that music-induced emotions can alter visually-induced emotions (e.g., Jeong et al., 2011), with arousal and pleasantness showing differential effects (Marin et al., 2012; Lee et al., 2017). Moreover, Marin et al. (2017) and Marin and Rathgeber (2022) employed facial targets because facial attractiveness is an important biological cue in mate choice (Currie and Little, 2009), in which overall sexual attraction is determined by a complex interplay of several physical, cognitive and social cues (Buss and Schmitt, 2019).

Misattribution of arousal (i.e., excitation transfer, Zillmann, 1983, see also Dutton and Aron, 1974; Foster et al., 1998) was identified by Marin et al. (2017) as a potential psychological mechanism through which music can affect mate choice (see also May and Hamilton, 1980). Musical primes varying in arousal and pleasantness were selected from the 19th-century piano repertoire. High-arousing musical excerpts were also more complex than low-arousing excerpts. Compared to a silent control condition, females gave higher facial attractiveness and dating desirability ratings in response to opposite-sex faces after musical priming, with high-arousing excerpts showing the largest effects. Conception risk did not significantly affect these ratings (but see Charlton, 2014). There were no significant effects in males. In their follow-up study, Marin and Rathgeber (2022) focused on musicality and modified the instructions accordingly. Participants were told that the musical excerpts were performed by the people shown on the photographs. A significant increase in facial attractiveness and dating desirability after musical priming was found in females, but no specific arousal/complexity effect. In males, dating desirability (but not attractiveness) ratings increased after musical priming. Ideally, studies on music and sexual selection should include only singles (as in Marin and Rathgeber, 2022, but unlike Marin et al., 2017) and only females that are not using hormonal contraception (as in both studies led by Marin).

Marin et al. (2017) and Marin and Rathgeber (2022) offered some insights into the psychological mechanisms by which instrumental music may affect sexual attraction in listeners. In both studies, a crossmodal priming paradigm was employed with the same stimulus materials but different instructions. One can thus conclude that excitation-transfer effects are clearly observable when musical primes and facial targets are not explicitly linked by the instructions, but not when primes and targets are linked. This suggests two possible (partly interwoven?) pathways by which music(ality) may affect partner choice: one route that is rather affect-based, and another that showcases the musician as someone having advanced motoric and expressive skills (Miller, 2000). Since arousal (affective route) and complexity (honest signal) are often interrelated in music (see Marin and Leder, 2013), further studies using different musical styles and experimental paradigms are necessary. Studies should also incorporate a wider range of physical mate cues (Groyecka et al., 2017), such as the human voice, and examine performer-listener interactions given recent observations suggesting intrasexual competition in human chorusing (Keller et al., 2023). Overall, Marin's findings are in agreement with Darwin's (1871, p. 880) claim that "the progenitors of man, either the males or females or both sexes, […] endeavoured to charm each other with musical notes and rhythm".

Focusing on musical creativity as a fitness indicator, Madison et al. (2018) studied multiple cues in mate choice and combined faces of three levels of attractiveness with musical excerpts of three levels of performance quality. The authors framed their research in the context of Darwin's sexual selection hypothesis and parental investment theory (Trivers, 1996). They tested female and male participants who looked at an opposite-sex face while listening to musical improvisations which were all played at the same tempo and in major mode. This minimized affective differences between the performance quality levels and thus facilitated the interpretability of the effects. Participants were asked to rate mate value (intelligence, health, social status and parenting skill) and mate preference scales (date, intercourse, short- and long-term relationship) as well as attractiveness. In general, improvisation skills increased all types of ratings with a few exceptions; however, facial attractiveness had a much larger effect than performance quality, and exerted a smaller influence on ratings among females than among males. Altogether, the results do not falsify the sexual selection hypothesis of music evolution.

Darwin (1871, p. 332) observed that in "most of the lower classes [non-mammals] the sounds produced by the males, serve not only to call but to excite or allure the female". At that time, evidence for Darwin's observation was lacking among mammals. Kreutz (1997) hypothesized that music may affect erotic relationships by intensifying perceptions and emotions in humans. Indeed, there is now empirical evidence for music's role in sexual arousal (Wan and Lalumière, 2017; van Bohemen et al., 2018; Tikka et al., 2022; but see Grewe et al., 2009) and sexual fantasies (Lehmiller, 2018). These findings may be interpreted as supporting the view that sexual selection plays a role in the evolution of musicality. In this context, one may be inclined to take the existence of love songs and its role in romantic pair bonding (Dukes et al., 2003; Hobbs and Gallup, 2011) as further evidence for sexual selection. However, romantic relationships (and pair bonding) between men and women, as we understand it nowadays, presumably did not exist in hunter-gatherer tribes and were probably not expressed in songs. Monogamous relationships only became the dominant model late in our history (perhaps around 10,000 years ago) when the development of agriculture considerably changed mating behavior (see Miller, 1998). Moreover, Brown (2000b) has argued that interactions between music and language, such as in songs with lyrics, appeared after music and language evolved as two distinct communication systems out of one common hominid referential emotive vocalization system. Therefore, we consider the study of love songs to be secondary when trying to address the possible roots of human musicality.

Other supportive evidence for music's role in sexual attraction stems from simulation studies (Werner and Todd, 1997; Van den Broek and Todd, 2009), studies investigating the influence of depicting musical instruments on men's profile pictures in social media (Tifferet et al., 2012, but see Wassiliwizky et al., 2023) and the role of music and musicianship in self-descriptions in the context of online dating (Lee et al., 2019). However, Bongard et al. (2019) reported that verbal profiles of musicians were not rated as more attractive than those of non-musicians, but raters who were musically interested found musicians attractive in private settings (see also Montoya et al., 2008). Chang et al. (2021) studied the effect of body sway in a speed dating paradigm with groovy background music and found that, compared to low-groove music, high-groove music led to an increased interest in meeting the partner again, suggesting that social bonding mechanisms based on groove and entrainment may be another route through which music may increase sexual attraction (see Savage et al., 2021). Interestingly, groovy music has been associated with heightened arousal (Bowling et al., 2019), implying a potential arousal-based mechanism. Another recent study suggests that the practice behavior of heavy metal guitarists may be related to status seeking and mate attraction (DeLecce et al., 2022).

5 Discussion

This review has shown that empirical evidence for music's role in sexual attraction has accumulated in the last decade, mostly stemming from behavioral studies focusing on listeners' perceptions and subjective responses. First, musicality, including mere visual indication of musical proficiency (Tifferet et al., 2012; Lee et al., 2019), has been demonstrated to be an attractive trait, especially among female listeners (Charlton, 2014; Madison et al., 2018; Marin and Rathgeber, 2022). Second, the emotional impact of music seems to enhance perceived attractiveness (Marin et al., 2017; Chang et al., 2021) and sexual arousal (Tikka et al., 2022) in listeners. However, a fully convincing argument for sexual selection based on behavioral measures would require demonstrating greater mating success among musically skilled individuals (Ravignani, 2018; see also Section 2), or at least, more frequent (and perhaps risky) sexual behavior. On the other hand, the role of sexual selection will only be completely refuted if the best available evidence (for instance, obtained from a cross-cultural meta-analysis) refutes every plausible sub-mechanism of sexual selection in both performers and listeners. It is possible that only a few mechanisms of sexual selection have significant explanatory power in the evolution of musicality.

The issue of sexual dimorphism in relation to sexual selection warrants further research (Varella et al., 2010, 2017, 2022). For instance, studies employing both female and male participants and depictions of opposite-sex faces have shown that males' ratings of female facial attractiveness are nearly impervious to music or cues of musicality, whereas females appear to be more sensitive to such cues (Marin et al., 2017; Madison et al., 2018; Marin and Rathgeber, 2022; see also Kaufman et al., 2016). The mutual mate choice model, which argues that sexual dimorphism is low among humans, although some sex differences remain, may help explain these results (Miller, 2013). Thus, the absence of significant sex differences in basic music perception skills (Bertolo et al., 2023) does not provide convincing evidence against sexual selection, since both sexes need to be able to perceive and evaluate aesthetic displays (Miller, 2001; Varella, 2023). In general, the current empirical evidence seems to be in line with Darwin (1871), who did not regard music as a sexual dimorphic trait.

Future challenges include the study of other facets of musicality besides instrumental music, such as singing (Grewe et al., 2009; Valentova et al., 2019; Keller et al., 2023), dance (Weege et al., 2015; Garfinkel, 2018; Fink et al., 2021), and beat synchronization (Ravignani, 2018). Different sexual selection mechanisms may have shaped these various aspects of musicality to different degrees. In this regard, it may be fruitful to work closely together with ethnomusicologists to collect meaningful cross-cultural data in laboratories as well as in the field. A strictly Western perspective will not be sufficient when studying the origins of music.

Another strand of research should explore in greater depth the underlying mechanisms by which music and musicality affect mate choice, with a particular emphasis on music-induced emotions. In the long term, this will offer insights into how affect and cognition interact in decision-making processes related to sexual behavior, which will be of interest to fields outside music psychology. At the moment, affective arousal appears to be the key player explaining how music affects sexual attraction. Arousal-based theories such as "misattribution of arousal" (Schachter and Singer, 1962), "excitation-transfer" (Zillmann, 1983) or the "arousal-as-information" framework (Storbeck and Clore, 2008) are helpful to explain some of the observed effects. Motivational theories, such as Berlyne's (1960) psychobiological model, which is still frequently cited in the field of empirical aesthetics (Marin, 2022), also consider arousal as vital in determining hedonic responses to different kinds of artworks including music. Nevertheless, the role of valence and more complex emotions (Clore, 1992; Angie et al., 2011; DeWall et al., 2016) in social judgments and decision-making regarding musicality and sexual attraction has yet to be explored in depth. When studying these decision-making processes during music listening, it will also be important to disentangle effects that are based on evaluations of musical abilities (performance quality or musical creativity) from emotion-based influences on sexual attraction.

Furthermore, the impact of musicality and music on different types of mate preferences (Buss and Schmitt, 2019) has not been sufficiently studied so far (but see Charlton, 2014; Madison et al., 2018). Although short-term mating behavior is most relevant for the theory of sexual selection, music activities may increase the quality of long-term relationships by creating intimacy between partners (see Kreutz and Feldhaus, 2023). Moreover, a broader spectrum of mate cues needs to be studied to get a better understanding of the relative importance of music-related cues, as well as other cues of human artisticality (Varella, 2021), creativity (Kaufman et al., 2016; Novaes and Natividade, 2023) and humor (Kaufman et al., 2008). Finally, future studies should account for cultural stereotypes related to musical styles (Zillmann and Azra, 1989), and consider music preferences and different types of musical proficiency in their research designs (Bongard et al., 2019).

Author contributions

MM: Conceptualization, Writing – review & editing, Writing – original draft. BG: Conceptualization, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. Open access funding provided by University of Vienna.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Angie, A. A., Connelly, S., Waples, E. P., and Kligyte, V. (2011). The influence of discrete emotions on judgement and decision-making: a meta-analytic review. *Cognit. Emot.* 25, 1393–1422. doi: 10.1080/02699931.2010.550751

Bachman, N., Palgi, Y., and Bodner, E. (2022). Emotion regulation through music and mindfulness are associated with positive solitude differently at the second half of life. *Int. J. Behav. Develop.* 46, 520–527. doi: 10.1177/01650254221131304

Beer, A., and Greitemeyer, T. (2019). The effects of background music on tipping behavior in a restaurant: a field study. *Psychol. Music* 47, 444–450. doi: 10.1177/0305735618755887

Beerli, P., and Edwards, S. V. (2002). When did Neanderthals and modern humans diverge? *Evol. Anthropol.* 11, 60–63. doi: 10.1002/evan.10058

Benítez-Burraco, A., and Nikolsky, A. (2023). The (co)evolution of language and music under human self-domestication. *Hum. Nat.* 34, 229–275. doi: 10.1007/s12110-023-09447-1

Berlyne, D. E. (1960). *Conflict, arousal, and curiosity*. New York, NY: McGraw-Hill Book Company.

Bertolo, M., Müllensiefen, D., Peretz, I., Woolley, S. C., Sakata, J., and Mehr, S. (2023). "Human music perception ability is not a sexually dimorphic trait." In *Proceedings of the Annual Meeting of the Cognitive Science Society*, eds. M. Goldwater, F. K. Anggoro, B. K. Hayes, and D. C. Ong (Vol. 45), 1823–31.

Bispham, J. C. (2009). Music's "design features": musical motivation, musical pulse, and musical pitch. *Music. Sci.* 13, 41–61. doi: 10.1177/1029864909013002041

Blacking, J. (1973). *How musical is man?* Seattle, WA: University of Washington Press.

Blood, A. J., and Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. USA* 98, 11818–11823. doi: 10.1073/pnas.191355898

Bongard, S., Schulz, I., Studenroth, K. U., and Frankenberg, E. (2019). Attractiveness ratings for musicians and non-musicians: an evolutionary-psychology perspective. *Front. Psychol.* 10:2627. doi: 10.3389/fpsyg.2019.02627

Bowling, D. L., Ancochea, P. G., Hove, M. J., and Fitch, W. T. (2019). Pupillometry of groove: evidence for noradrenergic arousal in the link between music and movement. *Front. Neurosci.* 12:1039. doi: 10.3389/fnins.2018.01039

Brown, S. (2000a). "Evolutionary models of music: from sexual selection to group selection" in *Perspectives in ethology: Evolution, culture, and behavior*. eds. F. Tonneau and N. S. Thompson (Boston, MA: Springer US), 231–281.

Brown, S., and Jordania, J. (2013). Universals in the world's musics. *Psychol. Music* 41, 229–248. doi: 10.1177/0305735611425896

Brown, S. (2000b). "The "Musilanguage" model of music evolution" in *The origins of music*. eds. N. J. Wallin, B. Merker and S. Brown (Cambridge, MA: A Bradford Book, MIT Press), 271–300.

Buss, D. M., and Schmitt, D. P. (2019). Mate preferences and their behavioral manifestations. *Ann. Rev. Psychol.* 70, 77–110. doi: 10.1146/annurev-psych-010418-103408

Buss, D. M., and Shackelford, T. K. (2008). Attractive women want it all: good genes, economic investment, parenting proclivities, and emotional commitment. *Evol. Psychol.* 6, 147470490800600–147470490800146. doi: 10.1177/147470490800600116

Chang, A., Kragness, H. E., Tsou, W., Bosnyak, D. J., Thiede, A., and Trainor, L. J. (2021). Body sway predicts romantic interest in speed dating. *Soc. Cogn. Affect. Neurosci.* 16, 185–192. doi: 10.1093/scan/nsaa093

Charlton, B. D. (2014). Menstrual cycle phase alters women's sexual preferences for composers of more complex music. *Proc. R. Soc. Lond. B Biol. Sci.* 281:20140403. doi: 10.1098/rspb.2014.0403

Charlton, B. D., Filippi, P., and Fitch, W. T. (2012). Do women prefer more complex music around ovulation? *PLoS One* 7:e35626. doi: 10.1371/journal.pone.0035626

Cirelli, L. K., Jurewicz, Z. B., and Trehub, S. E. (2020). Effects of maternal singing style on mother-infant arousal and behavior. *J. Cogn. Neurosc.* 32, 1213–1220. doi: 10.1162/jocn_a_01402

Clayton, M. (2016). "The social and personal functions of music in cross-cultural perspective" in *The Oxford handbook of music psychology*. eds. S. Hallam, I. Cross and M. Thaut (New York: Oxford University Press), 47–59.

Clore, G. L. (1992). "Cognitive phenomenology: feelings and the construction of judgment" in *The construction of social judgements*. eds. L. L. Martin and A. Tesser (Hillsdale, NJ: Erlbaum), 133–163.

Conard, N. J., Malina, M., and Münzel, S. C. (2009). New flutes document the earliest musical tradition in southwestern Germany. *Nature* 460, 737–740. doi: 10.1038/nature08169

Cook, T., Roy, A. R. K., and Welker, K. M. (2019). Music as an emotion regulation strategy: an examination of genres of music and their roles in emotion regulation. *Psychol. Music* 47, 144–154. doi: 10.1177/0305735617734627

Cross, I. (2001). Music, cognition, culture, and evolution. *Ann. N. Y. Acad. Sci.* 930, 28–42. doi: 10.1111/j.1749-6632.2001.tb05723.x

Croston, R., Branch, C. L., Kozlovsky, D. Y., Dukas, R., and Pravosudov, V. V. (2015). Heritability and the evolution of cognitive traits. *Behav. Ecol.* 26, 1447–1459. doi: 10.1093/beheco/arv088

Currie, T. E., and Little, A. C. (2009). The relative importance of the face and body in judgments of human physical attractiveness. *Evol. Hum. Behav.* 30, 409–416. doi: 10.1016/j.evolhumbehav.2009.06.005

Darwin, C. R. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.

Davis, A. C., and Arnocky, S. (2022). Darwin versus Wallace: esthetic evolution and preferential mate choice. *Front. Psychol.* 13:862385. doi: 10.3389/fpsyg.2022.862385

DeLecce, T., Pazhoohi, F., Szala, A., and Shackelford, T. K. (2022). Extreme metal guitar skill: a case of male–male status seeking, mate attraction, or byproduct? *Evol. Behav. Sci.* 18, 54–66. doi: 10.1037/ebs0000304

DeWall, C. N., Baumeister, R. F., Chester, D. S., and Bushman, B. J. (2016). How often does currently felt emotion predict social behavior and judgment? A meta-analytic test of two theories. *Emot. Rev.* 8, 136–143. doi: 10.1177/1754073915572690

Dissanayake, E. (2008). If music is the food of love, what about survival and reproductive success? *Music. Sci.* 12, 169–195. doi: 10.1177/1029864908012001081

Dukes, R. L., Bisel, T. M., Borega, K. N., Lobato, E. A., and Owens, M. D. (2003). Expressions of love, sex, and hurt in popular songs: a content analysis of all-time greatest hits. *Soc. Sci. J.* 40, 643–650. doi: 10.1016/S0362-3319(03)00075-2

Dunbar, R. (2004). "Language, music, and laughter in evolutionary perspective" in *Evolution of communication systems: A comparative approach*. eds. D. K. Oller and U. Griebel (Cambridge: MIT Press), 257–273.

Dutton, D. G., and Aron, A. P. (1974). Some evidence for heightened sexual attraction under conditions of high anxiety. *J. Pers. Soc. Psychol.* 30, 510–517. doi: 10.1037/h0037031

Evans, N. D., Juhl, J., Hepper, E. G., Wildschut, T., Sedikides, C., and Fetterman, A. K. (2022). Romantic nostalgia as a resource for healthy relationships. *J. Soc. Pers. Relat.* 39, 2181–2206. doi: 10.1177/02654075221075773

Fasano, M. C., Cabral, J., Stevner, A., Vuust, P., Cantou, P., Brattico, E., et al. (2023). The early adolescent brain on music: analysis of functional dynamics reveals engagement of orbitofrontal cortex reward system. *Hum. Brain Map.* 44, 429–446. doi: 10.1002/hbm.26060

Ferreri, L., Mas-Herrero, E., Zatorre, R. J., Ripolles, P., Gomez-Andres, A., Alicart, H., et al. (2019). Dopamine modulates the reward experiences elicited by music. *Proc. Natl. Acad. Sci. USA* 116, 3793–3798. doi: 10.1073/pnas.1811878116

Fink, B., Bläsing, B., Ravignani, A., and Shackelford, T. K. (2021). Evolution and functions of human dance. *Evol. Hum. Behav.* 42, 351–360. doi: 10.1016/j.evolhumbehav.2021.01.003

Fisher, M. L., and Candea, C. (2012). You ain't woman enough to take my man: female intrasexual competition as portrayed in songs. *J. Soc. Evol. Cult. Psychol.* 6, 480–493. doi: 10.1037/h0099238

Foster, C. A., Witcher, B. S., Campbell, W. K., and Green, J. D. (1998). Arousal and attraction: evidence for automatic and controlled processes. *J. Pers. Soc. Psychol.* 74, 86–101. doi: 10.1037/0022-3514.74.1.86

Fuentes-Sanchez, N., Pastor, R., Escrig, M. A., Elipe-Miravet, M., and Pastor, M. C. (2021). Emotion elicitation during music listening: subjective self-reports, facial expression, and autonomic reactivity. *Psychophysiology* 58:e13884. doi: 10.1111/psyp.13884

Gangestad, S. W., and Thornhill, R. (2008). Human oestrus. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 991–1000. doi: 10.1098/rspb.2007.1425

Garfinkel, Y. (2018). The evolution of human dance: courtship, rites of passage, trance, calendrical ceremonies and the professional dancer. *Camb. Archaeol. J.* 28, 283–298. doi: 10.1017/S0959774317000865

Garrido, S., du Toit, M., and Meade, T. (2022). Music listening and emotion regulation: young people's perspectives on strategies, outcomes, and intervening factors. *Psychomusicology* 32, 7–14. doi: 10.1037/pmu0000285

Gingras, B., Honing, H., Peretz, I., Trainor, L. J., and Fisher, S. E. (2015a). Defining the biological bases of individual differences in musicality. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 370, 20140092–20140090. doi: 10.1098/rstb.2014.0092

Gingras, B., Marin, M. M., Puig-Waldmuller, E., and Fitch, W. T. (2015b). The eye is listening: music-induced arousal and individual differences predict pupillary responses. *Front. Hum. Neurosci.* 9:619. doi: 10.3389/fnhum.2015.00619

Grewe, O., Nagel, F., Altenmüller, E., and Kopiez, R. (2009). Individual emotional reactions towards music: evolutionary-based universals? *Music. Sci.* 13, 261–287. doi: 10.1177/1029864909013002121

Grewe, O., Nagel, F., Kopiez, R., and Altenmuller, E. (2007). Listening to music as a re-creative process: physiological, psychological, and psychoacoustical correlates of chills and strong emotions. *Music. Percept.* 24, 297–314. doi: 10.1525/mp.2007.24.3.297

Groyecka, A., Pisanski, K., Sorokowska, A., Havlicek, J., Karwowski, M., Puts, D., et al. (2017). Attractiveness is multimodal: beauty is also in the nose and ear of the beholder. *Front. Psychol.* 8:778. doi: 10.3389/fpsyg.2017.00778

Hagen, E. H., and Hammerstein, P. (2009). Did Neanderthals and other early humans sing? Seeking the biological roots of music in the territorial advertisements of primates, lions, hyenas, and wolves. *Music. Sci.* 13, 291–320. doi: 10.1177/1029864909013002131

Harrison, M. A., and Hughes, S. M. (2017). Sex drugs and rock and roll: evidence supporting the storied trilogy. *Hum. Ethol. Bull.* 32, 63–84. doi: 10.22330/heb/323/63-84

Haselton, M. G., and Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence. *Hum. Nat.* 17, 50–73. doi: 10.1007/s12110-006-1020-0

Herget, A. K. (2021). On music's potential to convey meaning in film: a systematic review of empirical evidence. *Psychol. Music* 49, 21–49. doi: 10.1177/0305735619835019

Hobbs, D. R., and Gallup, G. G. Jr. (2011). Songs as a medium for embedded reproductive messages. *Evol. Psychol.* 9, 390–416. doi: 10.1177/147470491100900309

Honing, H., and Ploeger, A. (2012). Cognition and the evolution of music: pitfalls and prospects. *Top. Cogn. Sci.* 4, 513–524. doi: 10.1111/j.1756-8765.2012.01210.x

Honing, H., ten Cate, C., Peretz, I., and Trehub, S. E. (2015). Without it no music: cognition, biology and evolution of musicality. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 370:20140088. doi: 10.1098/rstb.2014.0088

Huron, D. (2001). Is music an evolutionary adaptation? *Ann. N. Y. Acad. Sci.* 930, 43–61. doi: 10.1111/j.1749-6632.2001.tb05724.x

Jeong, J. W., Diwadkar, V. A., Chugani, C. D., Sinsoongsud, P., Muzik, O., Behen, M. E., et al. (2011). Congruence of happy and sad emotion in music and faces modifies cortical audiovisual activation. *NeuroImage* 54, 2973–2982. doi: 10.1016/j.neuroimage.2010.11.017

Juslin, P. N. (2013). From everyday emotions to aesthetic emotions: towards a unified theory of musical emotions. *Phys Life Rev* 10, 235–266. doi: 10.1016/j.plrev.2013.05.008

Juslin, P. N., and Laukka, P. (2003). Communication of emotions in vocal expression and music performance: different channels, same code? *Psychol. Bull.* 129, 770–814. doi: 10.1037/0033-2909.129.5.770

Juslin, P. N., and Laukka, P. (2004). Expression, perception, and induction of musical emotions: a review and a questionnaire study of everyday listening. *J. New Music Res.* 33, 217–238. doi: 10.1080/0929821042000317813

Juslin, P. N., and Sloboda, J. (eds.). (2011). *Handbook of music and emotion: theory, research, applications*. Oxford: Oxford University Press.

Justus, T., and Hutsler, J. J. (2005). Fundamental issues in the evolutionary psychology of music: assessing innateness and domain specificity. *Music. Percept.* 23, 1–27. doi: 10.1525/mp.2005.23.1.1

Kalinowski, K., Kozłowska, A., Malesza, M., and Dariusz, P. D. (2021). Evolutionary origins of music. Classical and recent hypotheses. *Anthropol. Rev.* 84, 213–231. doi: 10.2478/anre-2021-0011

Kaufman, S. B., Kozbelt, A., Bromley, M. L., and Miller, G. R. (2008). "The role of creativity and humor in human mate selection" in *Mating intelligence: sex, relationships, and the mind's reproductive system*. eds. G. Geher and G. Miller (Mahwah, NJ: Erlbaum), 227–262.

Kaufman, S. B., Kozbelt, A., Silvia, P., Kaufman, J. C., Ramesh, S., and Feist, G. J. (2016). Who finds bill gates sexy? Creative mate preferences as a function of cognitive ability, personality, and creative achievement. *J. Creat. Behav.* 50, 294–307. doi: 10.1002/jocb.78

Keller, P. E., Lee, J., König, R., and Novembre, G. (2023). Sex-related communicative functions of voice spectral energy in human chorusing. *Biol. Lett.* 19:20230326. doi: 10.1098/rsbl.2023.0326

Killin, A. (2018). The origins of music: evidence, theory, and prospects. *Music Sci.* 1:205920431775197. doi: 10.1177/2059204317751971

Kleinman, K. (2015). Darwin and Spencer on the origin of music: is music the food of love? *Prog. Brain Res.* 217, 3–15. doi: 10.1016/bs.pbr.2014.11.018

Koelsch, S., Kasper, E., Sammler, D., Schulze, K., Gunter, T., and Friederici, A. D. (2004). Music, language and meaning: brain signatures of semantic processing. *Nat. Neurosci.* 7, 302–307. doi: 10.1038/nn1197

Kreutz, G. (1997). Musikrezeption zwischen Liebestraum und Love-Parade. Sexualität und Sinnlichkeit im Erleben von Musik. *Z. Medienpsychologie* 9, 293–311.

Kreutz, G., and Feldhaus, M. (2023). The influence of parent-child relationships on musical activity in the family: findings from a longitudinal panel study. *Music Sci.* 6:205920432211493. doi: 10.1177/20592043221149351

Krumhansl, C. L. (1997). An exploratory study of musical emotions and psychophysiology. *Can. J. Exp. Psychol.* 51, 336–353. doi: 10.1037/1196-1961.51.4.336

Lange, B. P., and Euler, H. A. (2014). Writers have groupies, too: high quality literature production and mating success. *Evol. Behav. Sci.* 8, 20–30. doi: 10.1037/h0097246

Lee, A. J., Jones, B. C., and Debruine, L. M. (2019). Investigating the association between mating-relevant self-concepts and mate preferences through a data-driven analysis of online personal descriptions. *Evol. Hum. Behav.* 40, 325–335. doi: 10.1016/j.evolhumbehav.2019.01.005

Lee, I. E., Latchoumane, C. F. V., and Jeong, J. (2017). Arousal rules: an empirical investigation into the aesthetic experience of cross-modal perception with emotional visual music. *Front. Psychol.* 8:440. doi: 10.3389/fpsyg.2017.00440

Lehmiller, J. J. (2018). *Tell me what you want: The science of sexual desire and how it can help you improve your sex life*. New York, NY: Da Capo Press.

Madison, G., Holmquist, J., and Vestin, M. (2018). Musical improvisation skill in a prospective partner is associated with mate value and preferences, consistent with sexual selection and parental investment theory: implications for the origin of music. *Evol. Hum. Behav.* 39, 120–129. doi: 10.1016/j.evolhumbehav.2017.10.005

Marin, M. M., and Bhattacharya, J. (2011). "Music induced emotions: some current issues and cross-modal comparisons" in *Music education*. eds. J. Hermida and M. Ferrero (Hauppauge, NY: Nova Science Publishers), 1–38.

Marin, M. M., Gingras, B., and Bhattacharya, J. (2012). Crossmodal transfer of arousal, but not pleasantness from the musical to the visual domain. *Emotion* 12, 618–631. doi: 10.1037/a0025020

Marin, M. M., and Leder, H. (2013). Examining complexity across domains: relating subjective and objective measures of affective environmental scenes, paintings and music. *PLoS One* 8:e72412. doi: 10.1371/journal.pone.0072412

Marin, M. M. (2022). "The role of collative variables in aesthetic experiences" in *The Oxford handbook of empirical aesthetics*. eds. M. Nadal and O. Vartanian (Oxford: Oxford University Press), 385–429.

Marin, M. M., and Rathgeber, I. (2022). Darwin's sexual selection hypothesis revisited: musicality increases sexual attraction in both sexes. *Front. Psychol.* 13:971988. doi: 10.3389/fpsyg.2022.971988

Marin, M. M., Schober, R., Gingras, B., and Leder, H. (2017). Misattribution of musical arousal increases sexual attraction towards opposite-sex faces in females. *PLoS One* 12:e0183531. doi: 10.1371/journal.pone.0183531

Ma, W., Fiveash, A., and Thompson, W. F. (2019). Spontaneous emergence of language-like and music-like vocalizations from an artificial protolanguage. *Semiotica* 2019, 1–23. doi: 10.1515/sem-2018-0139

May, J. L., and Hamilton, P. A. (1980). Effects of musically evoked affect on women's interpersonal attraction toward and perceptual judgments of physical attractiveness of men. *Motiv. Emot.* 4, 217–228. doi: 10.1007/BF00995420

McDermott, J., and Hauser, M. (2005). The origins of music: innateness, uniqueness, and evolution. *Music. Percept.* 23, 29–59. doi: 10.1525/mp.2005.23.1.29

Mehr, S. A., Krasnow, M. M., Bryant, G. A., and Hagen, E. H. (2021). Origins of music in credible signaling. *Behav. Brain Sci.* 44:e60. doi: 10.1017/s0140525x20000345

Miller, G. F. (2001). Aesthetic fitness: how sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bull. Psychol. Arts* 2, 20–25.

Miller, G. F. (2013). Mutual mate choice models as the red pill in evolutionary psychology: long delayed, much needed, ideologically challenging, and hard to swallow. *Psychol. Inq.* 24, 207–210. doi: 10.1080/1047840X.2013.817937

Miller, G. F. (1998). "How mate choice shaped human nature: a review of sexual selection and human evolution" in *Handbook of evolutionary psychology: Ideas, issues, and applications*. eds. C. Crawford and D. L. Krebs (Mahwah, NJ: Lawrence Erlbaum Associates), 87–129.

Miller, G. F. (1999). "Sexual selection for cultural displays" in *The evolution of culture*. ed. C. Power (Edinburgh: Edinburgh University Press), 71–91.

Miller, G. F. (2000). "Evolution of human music through sexual selection" in *The origins of music*. eds. N. Wallin, B. Merker and S. Brown (Cambridge, MA: MIT Press), 329–360.

Mithen, S. (ed.). (1998). *Creativity in human evolution and prehistory*. London: Routledge.

Montoya, R. M., Horton, R. S., and Kirchner, J. (2008). Is actual similarity necessary for attraction? A meta-analysis of actual and perceived similarity. *J. Soc. Pers. Relat.* 25, 889–922. doi: 10.1177/0265407508096700

Mori, K., and Iwanaga, M. (2021). Being emotionally moved is associated with phasic physiological calming during tonic physiological arousal from pleasant tears. *Int. J. Psychophysiol.* 159, 47–59. doi: 10.1016/j.ijpsycho.2020.11.006

Mosing, M. A., Verweij, K. J. H., Madison, G., Pedersen, N. L., Zietsch, B. P., and Ullen, F. (2015). Did sexual selection shape human music? Testing predictions from the sexual selection hypothesis of music evolution using a large genetically informative sample of over 10,000 twins. *Evol. Hum. Behav.* 36, 359–366. doi: 10.1016/j.evolhumbehav.2015.02.004

Müllensiefen, D., Gingras, B., Musil, J., and Stewart, L. (2014). The musicality of non-musicians: an index for assessing musical sophistication in the general population. *PLoS One* 9:e89642. doi: 10.1371/journal.pone.0089642

Navarro, J., Osiurak, F., Gaujoux, V., Ouimet, M. C., and Reynaud, E. (2019). Driving under the influence: how music listening affects driving behaviors. *Jove* 145:e58342. doi: 10.3791/58342

Nigst, P. R., Haesaerts, P., Damblon, F., Frank-Fellner, C., Mallol, C., Viola, B., et al. (2014). Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. *Proc. Natl. Acad. Sci. USA* 111, 14394–14399. doi: 10.1073/pnas.1412201111

North, A., and Hargreaves, D. (2008). *The social and applied psychology of music*. New York: Oxford University Press

Novaes, F. C., and Natividade, J. C. (2023). The sexual selection of creativity: a nomological approach. *Front. Psychol.* 13:874261. doi: 10.3389/fpsyg.2022.874261

Ogg, M., Sears, D. R. W., Marin, M. M., and McAdams, S. (2017). Psychophysiological indices of music-evoked emotions in musicians. *Music. Percept.* 35, 38–59. doi: 10.1525/mp.2017.35.1.38

Patel, A. D. (2008). *Music, language, and the brain*. New York: Oxford University Press.

Persico, G., Antolini, L., Vergani, P., Costantini, W., Nardi, M. T., and Bellotti, L. (2017). Maternal singing of lullabies during pregnancy and after birth: effects on mother-infant bonding and on newborns' behaviour. Concurrent cohort study. *Women Birth* 30, e214–e220. doi: 10.1016/j.wombi.2017.01.007

Pinker, S. (1997). *How the mind works*. New York: W.W. Norton & Company.

Prum, R. O. (2012). Esthetic evolution by mate choice: Darwin's really dangerous idea. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 367, 2253–2265. doi: 10.1098/rstb.2011.0285

Ravignani, A. (2018). Darwin, sexual selection, and the origins of music. *Trends Ecol. Evol.* 33, 716–719. doi: 10.1016/j.tree.2018.07.006

Renoult, J. P. (2016). "The evolution of aesthetics: a review of models" in *Aesthetics and neuroscience: scientific and artistic perspectives*. eds. Z. Kapoula and M. Vernet (Cham: Springer), 271–300.

Savage, P. E., Brown, S., Sakai, E., and Currie, T. E. (2015). Statistical universals reveal the structures and functions of human music. *Proc. Natl. Acad. Sci. USA* 112, 8987–8992. doi: 10.1073/pnas.1414495112

Savage, P. E., Loui, P., Tarr, B., Schachner, A., Glowacki, L., Mithen, S., et al. (2021). Music as a coevolved system for social bonding. *Behav. Brain Sci.* 44:e59. doi: 10.1017/s0140525x20000333

Schachter, S., and Singer, J. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychol. Rev.* 69, 379–399. doi: 10.1037/h0046234

Schafer, T., and Sedlmeier, P. (2011). Does the body move the soul? The impact of arousal on music preference. *Music. Percept.* 29, 37–50. doi: 10.1525/mp.2011.29.1.37

Scherer, K. R. (2009). The dynamic architecture of emotion: evidence for the component process model. *Cognit. Emot.* 23, 1307–1351. doi: 10.1080/02699930902928969

Sloboda, J. A., and O'Neill, S. A. (2001). "Emotions in everyday listening to music" in *Music and emotion: Theory and research*. eds. P. N. Juslin and J. A. Sloboda (Oxford: Oxford University Press), 415–429.

Sluming, V. A., and Manning, J. T. (2000). Second to fourth digit ratio in elite musicians: evidence for musical ability as an honest signal of male fitness. *Evol. Hum. Behav.* 21, 1–9. doi: 10.1016/S1090-5138(99)00026-4

Steffens, J. (2020). The influence of film music on moral judgments of movie scenes and felt emotions. *Psychol. Music* 48, 3–17. doi: 10.1177/0305735618779443

Storbeck, J., and Clore, G. L. (2008). Affective arousal as information: how affective arousal influences judgments, learning, and memory. *Soc. Personal. Psychol. Compass* 2, 1824–1843. doi: 10.1111/j.1751-9004.2008.00138.x

Stroebele, N., and de Castro, J. M. (2006). Listening to music while eating is related to increases in people's food intake and meal duration. *Appetite* 47, 285–289. doi: 10.1016/j.appet.2006.04.001

Tifferet, S., Gaziel, O., and Baram, Y. (2012). Guitar increases male Facebook attractiveness: preliminary support for the sexual selection theory of music. *Lett. Evolut. Behav. Sci.* 3, 4–6. doi: 10.5178/lebs.2012.18

Tikka, S. K., Garg, S., Pattojoshi, A., and Tikka, D. L. (2022). "Sax for sex": a brief narrative review exploring the music-sex connect. *J. Psychosexual Health* 4, 138–142. doi: 10.1177/26318318221088935

Trehub, S. E. (2003). The developmental origins of musicality. *Nat. Neurosci.* 6, 669–673. doi: 10.1038/nn1084

Trivers, R. L. (1996). *Parental investment and sexual selection*. Chicago, IL: University of Chicago Press.

Turk, M., Turk, I., and Otte, M. (2020). The Neanderthal musical instrument from Divje babe I cave (Slovenia): a critical review of the discussion. *Appl. Sci.* 10:1226. doi: 10.3390/app10041226

Ullén, F., Mosing, M. A., Holm, L., Eriksson, H., and Madison, G. (2014). Psychometric properties and heritability of a new online test for musicality, the Swedish musical discrimination test. *Pers. Individ. Dif.* 63, 87–93. doi: 10.1016/j.paid.2014.01.057

Valentova, J. V., Tureček, P., Varella, M. A. C., Šebesta, P., Mendes, F. D. C., Pereira, K. J., et al. (2019). Vocal parameters of speech and singing covary and are related to vocal attractiveness, body measures, and sociosexuality: a cross-cultural study. *Front. Psychol.* 10:2029. doi: 10.3389/fpsyg.2019.02029

Van Bohemen, S., Den Hertog, L., and van Zoonen, L. (2018). Music as a resource for the sexual self: an exploration of how young people in the Netherlands use music for good sex. *Poetics* 66, 19–29. doi: 10.1016/j.poetic.2017.12.001

Van Den Broek, E. M., and Todd, P. M. (2009). Evolution of rhythm as an indicator of mate quality. *Music. Sci.* 13, 369–386. doi: 10.1177/10298649090130021

van der Zwaag, M. D., Janssen, J. H., Nass, C., Westerink, J., Chowdhury, S., and de Waard, D. (2013). Using music to change mood while driving. *Ergonomics* 56, 1504–1514. doi: 10.1080/00140139.2013.825013

Varella, M. A. C. (2021). Evolved features of artistic motivation: analyzing a Brazilian database spanning three decades. *Front. Psychol.* 12:769915. doi: 10.3389/fpsyg.2021.769915

Varella, M. A. C. (2023). Nocturnal selective pressures on the evolution of human musicality as a missing piece of the adaptationist puzzle. *Front. Psychol.* 14:1215481. doi: 10.3389/fpsyg.2023.1215481

Varella, M. A. C., Ferreira, J. H. B. P., Cosentino, L. A. M., Ottoni, E., and Bussab, V. S. R. (2010). Sex differences in aspects of musicality in a Brazilian sample: adaptative hypotheses. *Cogn. Music. Arts* 4, 10–16.

Varella, M. A. C., Sterbova, Z., Bartova, K., Fisher, M. L., and Valentova, J. V. (2022). Evolution of artistic and athletic propensities: testing of intersexual selection and intrasexual competition. *Front. Psychol.* 13:925862. doi: 10.3389/fpsyg.2022.925862

Varella, M. A. C., Valentova, J. V., and Fernández, A. M. (2017). "Evolution of artistic and aesthetic propensities through female competitive ornamentation" in *The Oxford handbook of female competition*. ed. M. L. Fisher (New York, NY: Oxford University Press), 757–783.

Vidal-Cordasco, M., Terlato, G., Ocio, D., and Marín-Arroyo, A. B. (2023). Neanderthal coexistence with *Homo sapiens* in Europe was affected by herbivore carrying capacity. *Sci. Adv.* 9:eadi4099. doi: 10.1126/sciadv.adi4099

Wallin, N. L., Merker, B., and Brown, S. (2001). *The origins of music*. Cambridge, MA: MIT Press.

Wan, C., and Lalumière, M. L. (2017). Can music cue sexual arousal? *Can. J. Hum. Sex.* 26, 238–248. doi: 10.3138/cjhs.2017-0011

Wassiliwizky, E., Jacobsen, T., Heinrich, J., Schneiderbauer, M., and Menninghaus, W. (2017). Tears falling on goosebumps: co-occurrence of emotional lacrimation and emotional piloerection indicates a psychophysiological climax in emotional arousal. *Front. Psychol.* 8:41. doi: 10.3389/fpsyg.2017.00041

Wassiliwizky, E., Wontorra, P., and Ullén, F. (2023). How being perceived to be an artist boosts feelings of attraction in others. *Sci. Rep.* 13:18747. doi: 10.1038/s41598-023-45952-0

Weege, B., Pham, M. N., Shackelford, T. K., and Fink, B. (2015). Physical strength and dance attractiveness: further evidence for an association in men, but not in women. *Am. J. Hum. Biol.* 27, 728–730. doi: 10.1002/ajhb.22703

Werner, G. M., and Todd, P. M. (1997). "Too many love songs: sexual selection and the evolution of communication" in *Fourth European conference on artificial life*. eds. P. Husbands and I. Harvey (Cambridge, MA: MIT Press/Bradford Books), 434–443.

Wesseldijk, L. W., Lu, Y., Karlsson, R., Ullen, F., and Mosing, M. A. (2023). A comprehensive investigation into the genetic relationship between music engagement and mental health. *Transl. Psychiatry* 13:15. doi: 10.1038/s41398-023-02308-6

Whittall, H., Gradisar, M., Fitton, J., Pillion, M., and Kahn, M. (2023). Can cry tolerance be increased in mothers of infants with sleep problems, and why does it matter? A quasi-experimental study. *Sleep Med.* 107, 64–71. doi: 10.1016/j.sleep.2023.04.018

Worden, R. (2022). The evolution of language by sexual selection. *Front. Psychol.* 13:1060510. doi: 10.3389/fpsyg.2022.1060510

Zillmann, D., and Azra, B. (1989). Effects of associating with musical genres on heterosexual attraction. *Com. Res.* 16, 263–288. doi: 10.1177/009365089016002005

Zillmann, D. (1983). "Transfer of excitation in emotional behavior" in *Social psychophysiology: A sourcebook*. eds. T. Cacioppo and R. E. Petty (New York: Guilford), 215–240.

frontiers | Frontiers in Psychology

TYPE Hypothesis and Theory
PUBLISHED 23 April 2024
DOI 10.3389/fpsyg.2024.1336363

EDITED BY
Florin Dolcos,
University of Illinois at Urbana-Champaign,
United States

REVIEWED BY
Giuliana Lucci,
Università degli Studi Guglielmo Marconi, Italy
Marco Bilucaglia,
Università IULM, Italy

*CORRESPONDENCE
Tjeerd Jellema
✉ T.Jellema@hull.ac.uk

RECEIVED 10 November 2023
ACCEPTED 08 April 2024
PUBLISHED 23 April 2024

CITATION
Jellema T, Macinska ST, O'Connor RJ and Skodova T (2024) Social intuition: behavioral and neurobiological considerations.
Front. Psychol. 15:1336363.
doi: 10.3389/fpsyg.2024.1336363

Social intuition: behavioral and neurobiological considerations

Tjeerd Jellema*, Sylwia T. Macinska, Richard J. O'Connor and Tereza Skodova

School of Psychology and Social Work, University of Hull, Hull, United Kingdom

Social intuition is instrumental in bringing about successful human interactions, yet its behavioral and neural underpinnings are still poorly understood. We focus in this article on the automatic, involuntary, nature of social intuition, rather than on higher-level cognitive and explicit Theory-of-Mind processes (which contribute to rendering social intuition meaningful in real-life situations). We argue that social-affective implicit learning plays a crucial role in establishing automatic social intuition. These implicit learning processes involve associations between the perception of other's bodily articulations, concurrent events, and the consequences or outcomes in terms of subsequent actions, affective valences and visceral states. The traditional non-social implicit learning paradigms do not allow one to draw conclusions about the role of implicit learning processes in social intuition, as they lack these vital characteristics typically associated with human actions. We introduce a new implicit learning paradigm, which aims to fill these gaps. It targets agile, rapid, social-affective learning processes, involving cue contingencies with a relatively simple structure, unlike the very complex structures that underpin the traditional tasks. The paradigm features matching social and non-social versions, allowing direct comparison. Preliminary data suggest equal performance of TD (typically-developed) and ASC (autism spectrum conditions) groups on the non-social version, but impaired implicit learning in ASC on the social version. We hypothesize that this reflects an anomalous use of implicitly learned affective information in ASC when judging other people. We further argue that the mirror neuron mechanism (MNM), which is part of the Action Observation Network, forms an integral part of the neural substrate for social intuition. In particular as there are indications that the MNM supports action anticipation, and that implicitly learned information can trigger MNM activation, which both seem vital to a social intuition ability. The insights that can be derived from comparing the performances of TD and ASC individuals on (non)social implicit learning tasks, and the implications for the role of MNM activation, are discussed.

KEYWORDS

social intuition, implicit learning, mirror neuron mechanism, affective valences, bodily articulations, autism spectrum conditions, autistic traits, anticipation

1 Introduction

Successful socio-affective human interactions form the glue that binds society, yet we are only just beginning to unravel the underpinning neural and behavioral mechanisms. Typically-developed (TD) individuals differ greatly in their social interaction abilities, while many psychological and neuro-developmental conditions, and mental illnesses, are characterized by profound difficulties in social interaction. A clear example are individuals with autism spectrum conditions (ASC; Autism Spectrum Conditions, also called Autism Spectrum Disorders; DSM-V-TR, 2022). The juxtaposition of ASC and TD therefore has the potential to offer insight into the mechanisms and processes underpinning socio-affective interactions.

One fundamental requirement for successful interactions is the skill that allows one to make rapid assumptions about what actions others are likely to take and what their intentions, emotions and thoughts might be. These assumptions should be made in a fairly effortless, automatic, manner, without the involvement of any prolonged, deliberate and effortful reasoning. We commonly call this skill *social intuition*. Social intuition manifests itself as 'immediate insight', and enables the rapid, social decision-making necessary to successfully navigate the ever-changing socially interactive world (Bechara et al., 1997; Lieberman, 2000). Task demands and time-restraints during social interactions mean that there is simply no time available to consciously reflect on what judgment to make or action to take. Therefore, individuals who depend upon deliberate, effortful reasoning, are likely unable to keep up with the pace of interactions. This may cause them to quickly lag behind and feel inadequate in social interactions. We propose this happens in ASC.

Social intuition can be considered a subdivision of social cognition. Whereas social cognition generally is concerned with how people, both explicitly and implicitly, process and apply information about other people and social situations (Frith, 2008), social intuition is essentially limited to implicit, automatic, effortless, processes that help to steer one's behavior in social situations in an advantageous way (Lieberman, 2000). The topicality of the question of how we accomplish the complex task of navigating the social world is reflected by recent propositions for a 'second-person' or 'interactive' approach in social cognition and social neuroscience (Schilbach et al., 2013; Redcay and Schilbach, 2019). This approach typically abandons the traditional use of 2D displays (images and videos), and replaces this with real-world real-time scenarios involving live actors, which brings social intuition to the forefront.

There are three main parts to this article. The first part [2] focusses on the role of implicit learning in forming social intuition. Here we look at the main non-social implicit learning paradigms, and indicate why they are of limited relevance for social interaction [2.1]. These non-social paradigms are then contrasted to social implicit learning paradigms, involving affective valences and bodily articulations [2.2]. We examine whether automatic action anticipation – a crucial ingredient of social intuition – can be brought about by implicit learning [2.3], and compare the performance of individuals with ASC on social versus non-social implicit learning tasks [2.4]. We next look at recent developments that aim to incorporate affective valences and bodily articulations in implicit learning paradigms [2.5].

In the second part [3], we discuss future developments and introduce a new paradigm developed in our lab, where implicit learning is tested in a social version [3.1] and in a matching, non-social, version [3.2]. Preliminary results, interpretations, alternative explanations and relevance are discussed [3.3].

In the third part [4], we examine the neural basis of social intuition. We look in particular at the role the mirror neuron mechanism (MNM) may play in social intuition, and posit that action anticipation is implemented in the MNM, and, importantly, that action anticipation can be triggered by implicitly learned action cues [4.1].

2 Implicit learning as a means to acquire social intuition

It has been suggested that social intuition is supported by a toolbox of social learning heuristics (Hertwig et al., 2013), many of which are *implicit* in nature. This means that one is not aware that any learning has taken place, even though it clearly affects one's subsequent decision making. Implicit learning typically applies to knowledge about rule-governed complexities in the environment and received a lot of attention (Reber, 1989; Bargh, 1994; Cleeremans, 2011; Schilbach et al., 2013). Although implicit processing and implicit knowledge proved difficult to define (see Gómez et al., 2017, for a discussion), one or more of the following adjectives are typically used to describe it: unintentional, uncontrolled, goal-independent, automatic, stimulus-driven, unconscious, efficient, effortless, fast and inflexible (Shiffrin and Schneider, 1977). From this list it is clear that a number of different dimensions are involved. Rather than each dimension forming a necessary constituent, what may matter most for defining implicitness is their relative contribution (Bargh, 1994), with unawareness (Moors and De Houwer, 2006) and automaticity (De Houwer and Moors, 2012) probably the most cited features.

Explicit learning processes, which often involve a form of deliberate hypothesis testing, are described by the opposite adjectives: intentional, controlled, goal-dependent, deliberate, top-down driven, conscious, inefficient, effortful, slow and flexible. Implicit and explicit processes may operate independently (dual process operation, Kliemann et al., 2013), and may be based on different mechanisms. This is supported by findings that the underpinning neuronal circuits may be dissociable, with implicit tasks showing in particular activation in the striatum and basal ganglia (e.g., implicit sequence learning; e.g. Rauch et al., 1997), anterior cingulate cortex and cerebellum, and explicit tasks showing in particular activation of prefrontal and visual cortical areas (Aizenstein et al., 2004). The relevance of the implicit-explicit distinction has been introduced very effectively to the wider public by Kahneman (2011) in his book "Thinking, Fast and Slow".

2.1 Non-social implicit learning paradigms

Humans seem to have the capacity to extract, and use, knowledge they apparently have no conscious access to. It could be that this knowledge was initially acquired explicitly and consciously, but was subsequently forgotten. Yet, the knowledge did not vanish from the brain, and kept on exerting an unconscious influence on behavior and decision making. However, it could also be that the knowledge never reached consciousness in the first place, but was learned implicitly.

With respect to this latter route, the literature shows an abundance of implicit non-social learning studies, demonstrating that one can learn about the sequential structure or rule that governs non-social, artificial, stimuli presentations (such as dots or letters), without one being explicitly aware of this underlying structure or rule. These non-social implicit learning tasks typically require hundreds of trials to induce a learning effect. Often cited examples are the Serial Reaction Time (SRT) task and the Artificial Grammar Learning (AGL) task. In typical SRT tasks (Nissen and Bullemer, 1987) stimuli are presented in one of four quadrants on a screen, and participants need to give a speeded response that corresponds to the specific quadrant where the stimulus appeared. Even though participants show no awareness or knowledge about the sequence, they consistently improve their reaction times over the course of the task, suggesting they had unconsciously learned the underlying pattern. In AGL tasks (Reber, 1967), participants are first exposed to meaningless strings of letters (e.g., XMXTVM; XXTRM) that are structured by a hidden, complex, rule (i.e., an artificial grammar). If, in a subsequent test phase, participants are able to accurately judge whether new strings follow the artificial grammar or not, then that suggests that they implicitly learned the underlying grammar (Reber, 1967; Dienes and Scott, 2005). Crucially, participants who implicitly learned the grammar often claim to respond at random, or to rely on an intuition they cannot further explain (Dienes and Scott, 2005).

The processes of unconscious knowledge acquisition, through implicit/unconscious learning, that emerge from these implicit learning paradigms, have been proposed to affect human behavior not only in laboratory paradigms, but also in the real-world social domain (Hudson et al., 2012b; Jurchiș and Dienes, 2023). However, this poses some serious problems. The non-social, implicit learning paradigms, that measure the capacity to implicitly pick-up on complex regularities between artificial, meaningless stimuli (dots, isolated letters), may be of no value for social interactions nor for social cognition in general. Such stimuli have no social significance, and the very large number of repetitions required to learn the regularities may render it impractical to be relevant for social interactions (though situations are conceivable where exposure to social 'rules' results in implicit learning only after large number of repetitions). Last but not least, social interactions are characterized, and guided by, affective valences, and by attitudes and dispositions, associated with human actions. All of these are wholly missing in the non-social paradigms.

2.2 Social implicit learning paradigms: affective valences and bodily articulations

Greenwald and Banaji (1995) defined implicitly learned material as introspectively unidentified (or inaccurately *identified*) traces of past experience that mediate favorable or unfavorable feeling, thought, or action toward objects. This definition acknowledges the role of affective valences in implicit learning. It has been argued that for cognition to be fully effective, it is not enough that the agent is able to understand and predict developments in the environment, it must also care about them, it must *desire* certain types of outcomes and *shun* others (Cleeremans, 2011). In this view, emotions are computational tags that subserve and facilitate cognitive processes. This may be true not only for explicit learning but also, and maybe especially, for implicit learning. It has been shown that an affective valence gets attached to a stimulus also when that stimulus is not consciously recognized (Kunst-Wilson and Zajonc, 1980). These implicitly associated affective valences may well be essential to make the rapid, intuitive, decisions that are beneficial to the individual and ultimately support their survival (Cleeremans, 2011). This view, in which emotions are computational tags that subserve and facilitate cognitive processes, is somewhat reminiscent of Damasio's somatic marker hypothesis (Damasio, 1994).

During real-life social interactions, the relevant stimuli usually consist of the other's actions, gestures, facial expressions and vocalizations, i.e., bodily articulations of one sort or another. Picking up on regularities and contingencies between the occurrence of these bodily articulations, contextual cues, and the immediate consequences (in terms of subsequent actions and/or subsequent reward/punishment) is an important source for implicit learning about others. Bodily articulations and affective valences thus seem necessary ingredients in any future implicit social learning paradigm.

There are a few cases where an attempt was made to include the social domain in an implicit learning paradigm (e.g., Brown et al., 2010; Travers et al., 2013). However, in these cases, the social nature of the animate objects was not pertinent to the paradigm and could just as well have been replaced by inanimate objects (i.e., affective valences, attitudes and dispositions played no part). One striking example of implicit social learning though was reported by Bayliss and Tipper (2006), who found that participants who had been presented with different actors who either consistently looked at, or away from, the location where a target would appear, subsequently judged those actors that had looked away from the target as the least 'trustworthy' and those who had looked at the target as the most 'trustworthy'. Crucially, in a debrief, participants did not recall any actor-gaze-cue contingencies, suggesting the contingencies had *implicitly* affected their social judgments. A further interesting finding was that this effect correlated negatively with the participants' scores on the Autism Quotient (AQ; Baron-Cohen et al., 2001).

2.3 Anticipation of others' actions based on implicitly learned cues

A social intuition, revealing itself as a sudden insight, inclination or drive relating to another individual, is typically prompted by the observation of an action or bodily articulation performed by that individual. However, it would be even more advantageous if one would be able to anticipate the other's action and then for that anticipation to prompt the intuition. That would save precious time, which can be used to prepare one's response in accordance with the intuition, or to coordinate one's own actions with those of others (Csibra, 2008). Especially in the fast-paced social interactions, this would be very beneficial. The automatic anticipation of others' actions is therefore thought to be an essential building block of social intuition (Hudson et al., 2009, 2012a; Krol et al., 2020). But what could be the source of such an anticipation, what could it be based on? First of all, actions typically do not occur in isolation, but in chains, where one sub-action is immediately followed by another sub-action and so on, resulting in an action-chain that serves a purpose (achieves a goal). Reaching out for a cup of coffee, bring it to the mouth, take a gulp and place the cup back. Once the first action of the chain started, it is able to trigger the entire action-chain almost instantaneously, like a row of falling dominos, unfolding ahead of real-time developments, and thus allowing the observer a glimpse of the future. The triggering event could also precede the action, it could for example be formed by the other's initial attention being directed at the object (Jellema et al., 2000). In general, others' actions seldom commence unheralded, they usually are foreshadowed by cues, which can be action cues (as above) or originate in the environment. Environmental/contextual cues can be artificial and explicit, such as a pedestrian traffic light jumping to green (the person waiting is expected to start walking), but can also be subtle and implicit.

Especially in social interactions, cues tend to be subtle and implicit (Amso and Davidow, 2012). Here, learning opportunities are often not explicit, as the learned cue-action contingencies may not reach consciousness (Monroy et al., 2019). The observer may remain completely unaware that any knowledge has been acquired, but the cue will nevertheless induce automatic anticipations in the observer regarding others' upcoming actions (Braukmann et al., 2017; Monroy et al., 2019). For example, when someone slightly moves in their chair in preparation to stand up, or slightly raise their hand when they are about to say something. Or when a nurse immediately sees what the patient wants to do, or a flight attendant immediately gauges that a passenger is going to cause trouble. Their insights are based on the automatic interpretation of a constellation of often simultaneously occurring cues. However, when one would ask the nurse or flight attendant how they reached their judgment, they may not even be able to recall the exact cues, they just 'saw' it. Nevertheless, a lot of implicit learning must have taken place before they were able to pick up on the relevant cues and then just 'saw' it (a naïve observer would have been oblivious). Without this implicit learning ability, other's actions would indeed often come unheralded, with the potential to surprise and bewilder any observer. This is, however, exactly how individuals with ASC, who arguably lack social intuition, often describe their experiences of others' actions. For them, deciphering the intended meaning of such actions is often anything but effortless and automatic.

2.4 Implicit learning in autism

ASC is a pervasive neurodevelopmental condition characterized by atypicality in social communication, impaired social development, and stereotypical, repetitive behaviors, often associated with obsessive interests and a lack of empathy (DSM-V-TR, 2022). Symptom severity varies hugely in ASC; three levels are identified based on severity and need of support. Already at Level 1 (previously called high-functioning autism), which is the least severe level with normal IQ distribution and no, or limited, need for support, the difficulties in social and emotional domains are marked. Intriguingly, it has been suggested that the deficits in the social domain that characterize ASC may have their roots in impairments in implicit (spontaneous) processing, with relatively intact explicit (deliberate) processing (Jellema et al., 2009; Senju et al., 2009; Schilbach et al., 2012). These ideas align with the Dual Process Theory of Autism (Evans, 2003), which proposes a dominance of deliberative (Type 2 processing) over intuitive (Type 1) processing. This proposition seems plausible, as in the social domain it is especially the quick and intuitive interpretation of others' non-verbal behavior that is problematic in ASC. However, studies aimed specifically at finding out whether implicit learning is impaired in ASC concluded that it is intact (e.g., Gordon and Stark, 2007; Barnes et al., 2008; Brown et al., 2010; Nemeth et al., 2010; Foti et al., 2015). Crucially though, all these studies had one important limitation in common: they focused exclusively on implicit learning in the *non-social* domain, using tasks involving probabilistic sequence rules. The social domain, where implicit learning relies on affective valences associated with the stimuli, and abstract concepts such as dispositions and intentions, was not incorporated. It may well be that different mechanisms are at play in the implicit learning of social, as compared to non-social, information.

2.5 Recent advances in the study of social implicit learning

Recently, a few studies aimed to specifically address the limited relevance of the non-social learning paradigms for social interactions (Norman and Price, 2012; Zhang et al., 2020; Costea et al., 2023; Jurchis et al., 2023; Jurchiş and Dienes, 2023). For example, Jurchis et al. (2023) took the approach to try and 'socialize' the traditional Artificial Grammar Learning (AGL) task. In the traditional AGL task, strings of meaningless letters are presented in the acquisition phase. In Jurchis et al. (2023), these strings of letters were replaced by strings of emotional facial expressions (all faces in one and the same string belonged to the same identity). As in the traditional AGL task, the strings of faces followed a hidden grammar, determining a number of specific sequences in which the faces were presented. In this way, Jurchis and colleagues were able to subject their implicit social learning paradigm to the same rigorous methods and principles that govern non-social implicit learning paradigms. At the start of the acquisition phase, participants were told that they had to remember the stimuli in each string. At the start of the test phase, they were told that the sequences in which these stimuli were presented had actually been specified by a complex set of rules, and that their task was to determine whether new test strings followed these rules or not. The number of repetitions of strings in the acquisition phase was also dramatically reduced compared to the non-social equivalent. In the test phase, where participants indicated whether the new strings followed the rule or not, in 70.6% of the trials they reported that their judgments were based on implicit/unconscious knowledge (the participants indicated that the remaining judgments were based on explicit knowledge). The implicit/unconscious judgments turned out to be correct in 58.2% of trials, which was significantly above-chance. In a further experiment in Jurchis et al. (2023), and also in Jurchiş and Dienes (2023), the same paradigm was used but with stimuli consisting of strings of martial art poses. These poses were 'social' in that human beings were presented displaying meaningful bodily articulations, yet (presumably) lacking in emotional valence. Similarly, in 67.5% of the trials, participants attributed their responses to unconscious knowledge, and in 57.5% of these latter trials the correct answer was given, again significantly above-chance.

Thus, implicit learning could be induced using social stimuli with relatively small numbers of repetitions, both when affective valences were associated with these stimuli and when not. However, these paradigms still do not resemble the patterns and types of stimuli that characterize real social situations, nor are emotional, motivational and interactive aspects of real social situations included. A few issues in particular spring to mind when considering the relevance of these tasks for daily-life social intuition. (i) While emotional facial expressions are highly relevant for social interactions, the simultaneous presentation of multiple facial expressions belonging to one and the same individual is impossible to encounter in real-life. Although the task recruits emotional processes, it is not done in an ecologically meaningful way. (ii) The participants were instructed to direct their attention to the very stimuli whose appearance was specified by the hidden rules. In daily-life interactions, the contingencies/regularities between bodily cues and their consequences typically do not form the focus of attention. Rather, attention may be focused on the joint activity (e.g., a conversation) one is engaged in, while the accompanying bodily cues that trigger anticipations may very well not be noted consciously. It is therefore unclear to what extent participants' behavior in this task informs about what people can learn from regularities/contingencies in real-life situations.

3 Future developments in implicit social/affective learning paradigms

In a series of recent experiments, Macinska and Jellema used a new implicit learning paradigm, designed to be particularly relevant for real-world social interaction (Macinska et al., 2015a,b; Macinska and Jellema, 2016; Macinska, 2019). The core paradigm was developed in Hudson et al. (2012b). The implicit social learning induced by this paradigm is characterized by rapid, agile, incidental processes that track relatively low order stimulus combinations, rather than slower processes that track very complex sequences and combinations, as in the traditional implicit learning paradigms. It requires a relatively small number of repetitions (about 10) to induce implicit learning effects, and allows to specifically compare participant's abilities for *social* versus *non-social* implicit learning. With respect to the latter, a non-social paradigm was designed that matched the social paradigm, as far as possible, in terms of the number of cues, internal structure and difficulty-level. This direct comparison is important as there is still a large gap in our knowledge about the extent to which the distinction between the social and non-social domain is relevant. Thus, in both paradigms a specific *contingency* between three different cues had to be learned. The main difference was, however, that implicit learning in the social paradigm crucially depended on affective valences, which were absent in the non-social paradigm, where learning depended purely on stimulus contingencies. The social cues were deliberately chosen for being straightforward and simple, so that ASC participants should not experience problems in deciphering their meaning. This was done to ensure that possible difficulties in implicit learning of the social contingencies cannot be attributed to difficulties with representing the social information *per se*.

Importantly, in the acquisition phases of both paradigms, contingencies rather than probabilities, have to be learned. That is, a rule determined specific contingencies between coordinated changes in the appearances of three distinct cues (each with two levels). The specific appearance of the level of one cue can be predicted with 100% certainty on the basis of the appearances of the levels of other two cues. It should be noted that in these paradigms, the participant is asked to simply watch the video-clips; there was no attempt to draw their attention to certain stimuli and they were not given a task to do. The acquisition phase was rather short (4 min), so they should be expected to maintain attention throughout that period.

3.1 Social version

3.1.1 Acquisition phase

In the social version, the three cues were: dynamic facial emotional expressions (levels: happiness vs. anger), gradual eye gaze shifts (levels: toward vs. away), and identity (levels: identity A vs. identity B). The advantage of using dynamic facial expressions is that they are more ecologically-valid (Jellema et al., 2011; Palumbo and Jellema, 2013; Palumbo et al., 2015; Sato et al., 2019). Participants were presented with short video clips (2 s) depicting the frontal face view of an actor (agent A or agent B; Figure 1). Their facial expressions and gaze directions changed smoothly over the course of the clips, displaying a natural facial movement. Fifty percent of trials showed actor A, the other 50% actor B, in random order. Actor A started with a happy expression looking straight ahead (at the observer), which then gradually morphed into an angry expression, while simultaneously the eye direction gradually moved away from the observer (so that in the final frame the actor looked angry away from the observer). The clips were also played backwards an equal number of times. Thus, it can be said that agent A had a positive disposition toward the observer. Agent B started with a happy expression looking away from the observer, which gradually morphed into an angry expression, while simultaneously the eye direction gradually moved toward the observer (clips were also played backwards an equal number of times). Actor B thus had a negative disposition toward the observer. Importantly, both actors smiled and frowned for exactly the same amount of time and looked at, and away from, the observer for exactly the same amount of time. This was to ensure that the actor's pro- or anti-social disposition toward the observer could only be learned on the basis of the specific combination of two cues linked to an identity; the agent's disposition could not be learned on the basis of each cue on its own. Too many repetitions meant most participants would detect the contingency (i.e., explicit learning), while with too few repetitions no implicit learning might take place.

3.1.2 Test phase

In the subsequent test phase, an indirect measure was used to find out whether any implicit learning had taken place. This measure involved a morph of the facial expressions of the two identities A and B, flanked by the original neutral faces of these two identities. The morphed identity was composed of 60% of the maximally smiling actor A and 40% the maximally smiling agent B (happy morph), and then progressed in steps of 5% toward 40% of the maximally smiling actor A and 60% the maximally smiling agent B. The same procedure was followed for the frowning actors A and B. Participants had to indicate for each morphed identity whether it resembled more closely agent A (who had a positive disposition toward the observer) or agent B (who had a negative disposition toward the observer). The rationale was that when participants had implicitly learned that identity A had a positive, and identity B a negative, disposition toward them, then they would be more likely to judge the smiling morph (containing 50% of A and 50% of B, both smiling maximally) as more similar to identity A, and the frowning morph (containing 50% of A and 50% of B, both frowning maximally) as more similar to identity B. This is expected, as, intuitively, they would associate identity A with a positive, and identity B with a negative, valence.

Whether or not the participant had consciously detected the cue-identity contingencies was determined in a short debrief session, in which a series of questions were asked probing any awareness of the contingencies. Participants who had detected the contingencies were removed from the analysis.

3.2 Non-social version

3.2.1 Acquisition phase

Two different shapes, a square and a circle, were used as the equivalent of the two identities A and B. The color of these objects

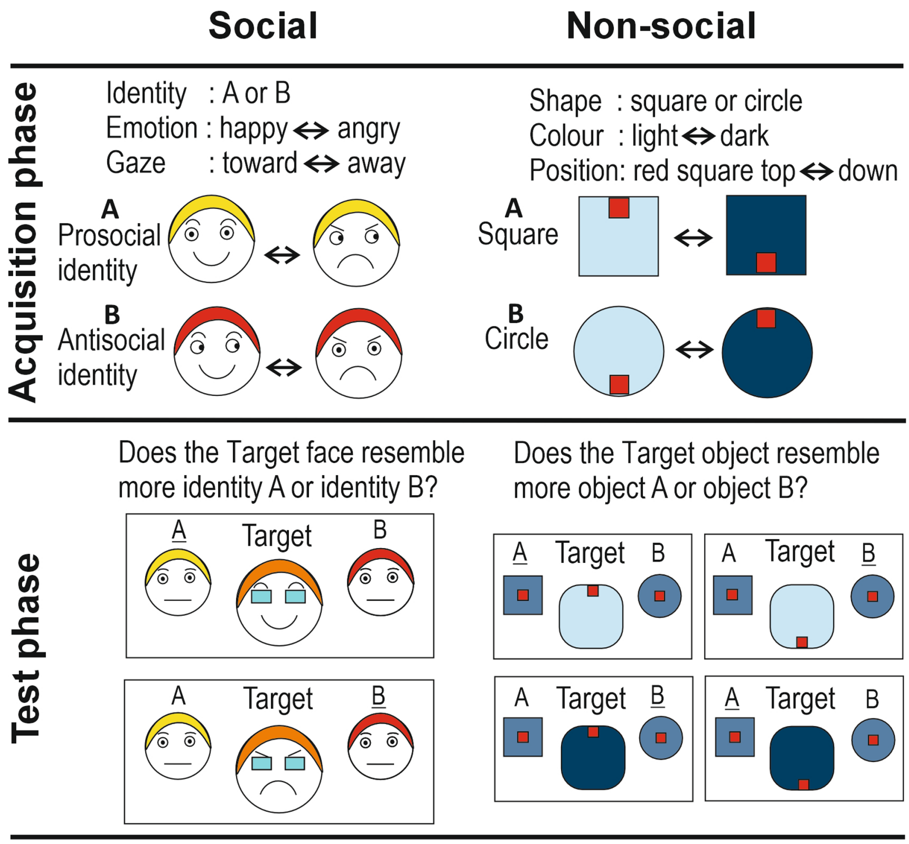


FIGURE 1
Schematic representation of the social and non-social implicit learning paradigms. The social identities are shown with differently colored hair for the purpose of illustrating their different identities. Responses in the Test phase ('A' and 'B') that reflect correct implicit learning are underlined.

– light blue or dark blue – was used as the equivalent of facial expressions of joy and anger, respectively. Therefore, a smooth dynamic change from light-blue to dark-blue, and vice versa, served as the equivalent of the changes in facial expression between joy and anger. A small red object positioned at the top or bottom position inside the bigger blue object, served as the equivalent of gaze direction (toward and away, respectively), while the dynamic, smooth up-or down-ward movement of this red object within the larger blue object served as the equivalent of the change in eye gaze direction. Vertical, rather than horizontal, movements were chosen to avoid interpretation of the small red objects as eyes, which might bestow the stimulus with animacy. Half of the clips started with the light-blue square, with the small red object at the top, which then gradually morphed into a dark-blue square with the small red object at the bottom (also played backwards). The other half of the clips started with the light-blue circle with the small red object at the bottom, which gradually moved into a dark-blue circle with the small object at the top (also played backwards).

3.2.2 Test phase

The nonsocial test phase was, as far as possible, equivalent to its social counterpart: morphs of the square and circle were presented (in 5% steps), in either a dark-blue (≈ anger) or light-blue (≈ happy) color, with the small red object shown at the top, or bottom, of this morphed object (producing four different morph configurations; see Figure 1, Test phase nonsocial). Target objects were flanked by the two original objects, which were shown in a color that was exactly midway the light-and dark-blue colors of the Acquisition phase (≈ neutral expression, midway happy and angry). Participants had to indicate whether the target object resembled more closely object A or object B. The rationale was that when participants had implicitly learned the specific contingencies, then they would judge the morphed target object to be more similar to a circle if the little red object was *(i)* at the top of the dark-blue target object, or *(ii)* at the bottom of the light-blue target object. Similarly, they would judge the target as more similar to a square if the small red object was at the top of the light-blue target, or at the bottom of the dark-blue target. As in the social condition, a debrief was held in which questions probed awareness of the stimulus contingencies. This showed that, similar to the social version, none of the participants had detected the stimulus contingencies.

In principle, this paradigm is open to a simpler type of learning, namely *perceptual* learning. That is, it could be that participants explicitly remembered the perceptual image of for example agent A with a smile and forward directed gaze. When, in the test phase, the morphed target is shown with a smile and eyes directed forward, then this could trigger the perceptual image of agent A with a smile looking forward. This would mean that the participant could give the correct response ('agent A') without having implicitly learned that agent A holds a positive disposition toward the observer. To avoid this possibility, the morphed target of the test phase was shown with the eyes covered by dark sunglasses obscuring visibility of eye gaze direction (Figure 1; note that the dark sunglasses did not prevent the morphed agent from expressing a disposition).

3.3 Preliminary results and hypotheses for future studies

We present here unpublished results based on 61 TD individuals who performed the Social task and on 65 participants who performed the Nonsocial task (37 of them performed both tasks; Social task: Age, M = 21.5, SD = 5.6; 25 males; Nonsocial task: Age, M = 20.7, SD = 4.7; 22 males; Figure 2). Two-way repeated measures ANOVAs were performed on the participants' judgments in both tasks. In the Social task, the two factors were Disposition (two levels: negative disposition or anti-social vs. positive disposition or pro-social) and Proportion (five levels: proportions of agents A and B contained in the Target face, ranging from 60%A/40%B, to 40%A/60%B, in steps of 5%). The main effect of Disposition was significant [$F(1, 60) = 8.2$, $p = 0.006$, $\eta_p^2 = 0.12$], reflecting that smiling Target faces were judged to resemble more the agent with the pro-social than the agent with the anti-social disposition, while frowning target faces were judged to resemble more the agent with anti-social than with pro-social disposition. The main effect of Proportion was also significant [$F(4, 240) = 32.7$, $p < 0.001$, $\eta_p^2 = 0.35$]. The Disposition by Proportion interaction effect was non-significant [$F(4, 240) = 0.99$, $p = 0.42$, $\eta_p^2 = 0.016$]. In the Non-social task, the two factors were Object (two levels: square vs. circle) and Proportion (five levels: proportions of objects A and B contained in the Target object, changing in steps of 5%). A similar pattern emerged as for the Social task, with significant main effects for Object [$F(1, 64) = 41.6$, $p < 0.001$, $\eta_p^2 = 0.39$] and Proportion [$F(4, 256) = 15.9$, $p < 0.001$, $\eta_p^2 = 0.20$], and no significant interaction effect [$F(4, 256) = 0.83$, $p = 0.51$, $\eta_p^2 = 0.013$]. Thus, in both tasks, significant implicit learning effects were found.

Since the participants' Autism Quotient scores (AQ; Baron-Cohen et al., 2001) had also been measured, we further explored any influence of AQ scores on implicit learning ability. AQ scores indicate the extent to which someone possesses autistic-like traits (ranging from 1 to maximally 50; higher scores reflecting a higher extent of autistic-like traits). Previous work indicated that the TD samples scoring low and high on the AQ may perform significantly different on social cognition tasks (Burnett and Jellema, 2013; Macinska and Jellema, 2022). The 61 TD individuals who performed the Social task had a mean AQ score of 17.6 (SD = 6.8, range 5 to 32); the 65 individuals who performed the Non-social task had a mean AQ score of 18.0 (SD = 6.5, range 7 to 32). To explore the hypothesis that autistic traits have a differential influence on implicit social/affective learning versus non-social learning, we computed the Pearson correlation coefficient to assess the linear relationship between AQ scores and a measure of implicit learning for both the Social and Nonsocial tasks. For the Social task, this measure was defined as the difference between the scores obtained for the 50%A/50%B frowning and smiling Targets. For the Nonsocial task, this measure was the difference between the 50%A/50%B light-blue and dark-blue colored Targets. Intriguingly, there was a significant negative correlation for the Social task [$r(62) = -0.36$, $p = 0.004$, two-tailed], indicating that autistic traits influenced the social/affective implicit learning ability (individuals having more traits being worse at it), while there was no significant correlation for the Nonsocial task [$r(62) = -0.052$, $p = 0.69$, two-tailed], indicating that autistic traits did not influence the nonsocial implicit learning ability. Future experiments will test individuals with ASC on these tasks. Our hypothesis is that the trend described above showing poorer implicit social/affective learning in the TD individuals with higher AQ scores, will become more prominent in individuals with ASC, while implicit learning in the nonsocial task will remain unaffected by ASC (Figure 2).

This outcome would suggest that a failure of the ASC group to implicitly learn in the social condition would not be due to an inability to implicitly learn cue contingencies *per se* (they are hypothesized to perform as well as the TD participants in the non-social condition), but may be related to an impairment to learn implicitly on the basis of affective valences.

A possible alternative explanation for the results, which does not assume an impairment in implicit affective learning in individuals high in autistic traits, is anomalous monitoring of the other's eye gaze. If these participants would avoid looking at the agent's eyes, or would avoid looking at direct gaze, then that would have repercussions for learning of the contingencies. Therefore, the scanning patterns of these facial expressions were examined in both TD and ASC groups in a separate study (Macinska et al., 2023). The study focused on eye-tracking using visual stimuli identical to those described here, but did not involve a test for implicit social learning. It revealed that both the TD and ASC groups spent most of their time fixating the agent's eyes, irrespective of gaze direction, which renders this explanation unlikely.

Another alternative explanation might be that individuals with low and high AQ scores differed in their memory for the facial expressions for particular gaze directions (i.e., an interaction between expression and gaze). For example, if the individuals high in autistic traits were poor in remembering facial expressions of anger when the gaze was directed at them, but were fine with remembering expressions of anger with gaze directed away, then that might go some way in explaining the results. However, in a study specifically addressing memory for facial expressions and possible modulation by gaze direction, using identical visual stimuli (Macinska and Jellema, 2022), autistic participants remembered the facial expressions of previously encountered persons as well as TD participants, without any interaction effects with gaze direction. Note that implicit learning was not measured in Macinska and Jellema (2022). Thus, this explanation can also be excluded, leaving the impaired implicit social-affective learning explanation as a viable option.

It is further possible that the agent's positive affect directed at the observer acted as a reward, which might have facilitated implicit learning. Such an effect would then be expected to be less pronounced in individuals who are somehow less susceptible to social rewards. It has been argued that individuals with ASC might possess a lowered ability to implicitly associate a reward value to a social stimulus, resulting in reduced social motivation (Dawson et al., 2005; Chevallier et al., 2012; Panasiti et al., 2015). Remarkably, these processes may be influenced by gender. In an fMRI (functional magnetic resonance imaging) study, Lawrence et al. (2020), using an instrumental implicit learning task, found reduced sensitivity to social reward (i.e., smiling faces) in frontostriatal and limbic structures in boys, but not in girls,

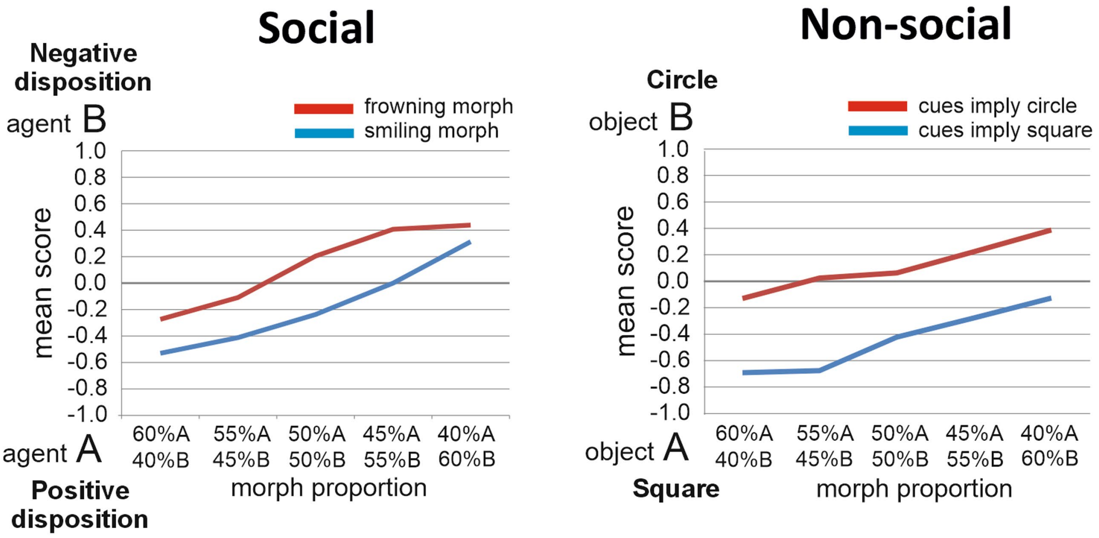


FIGURE 2
Task performance. The judgments made by TD individuals regarding the morphed target stimuli are presented for the Social implicit learning task (left panel) and for the Non-social implicit learning task (right panel).

with ASC. Reduced sensitivity to social reward in individuals high in autistic traits could in principle have contributed to our results. However, the majority of the participants in that group were female and thus, presumably, were sensitive to social reward.

Finally, it is possible that the presentation of dynamic facial expressions might have biased against implicit learning in individuals high in autistic traits, as it has been reported that the perception of dynamic, but not static, facial expressions, reduced activity in the amygdala and fusiform gyrus in ASC individuals (Pelphrey et al., 2007). However, the clips' initial and final static frames, presented for 750 ms each, were most informative for implicit learning about the agent's disposition, and we therefore do not expect this to be a major factor.

Which aspects of social intuition, as we defined it, does the newly designed task tap into? We described the social intuition ability as 'the skill that allows one to make rapid, assumptions about what actions others are likely to take and what their intentions, emotions and thoughts might be'. We further argued that this is mainly achieved through implicit learning of regularities and contingencies between bodily articulations, contextual cues, and the immediate consequences (in terms of subsequent actions and/or reward/punishment)'. The ability purportedly measured by the current task supports the sub-part of social intuition concerned with unconsciously associating a positive or negative valence with a particular identity on the basis of the implicit learning of specific contingencies between bodily articulations performed by that identity. In the new paradigm, the main bodily articulation consisted of a gradual change of an angry facial expression into a happy one, or vice versa. A change into a happy expression, however, does not necessarily result in the agent having a positive disposition toward the observer. For that to happen, the change in facial expression needed to be accompanied by another bodily articulation: a simultaneous change in gaze direction toward the observer (a change in opposite direction would not have led to a positive disposition toward the observer).

4 Neural basis of social intuition

The neural basis of social cognition has been the subject of extensive investigation, largely focusing on the deliberate, conscious, social cognitive processes (e.g., Frith, 2007; Adolphs, 2009). However, the neural basis of specifically social intuition, which is largely automatic and unconscious in nature and comprises of processes leading to decisions, responses and insights that are predominantly based on the perception of others' bodily articulations, has received much less attention. Hence, the current state of knowledge of the neural basis of social intuition is limited (*cf.* Wachowicz, 2020).

We posit here that the neural basis of social intuition may be linked to one of the key functions attributed to the mirror neuron mechanism (MNM; Rizzolatti and Craighero, 2004). The MNM 'matches' the visual description of another's bodily articulation or action (either visually perceived or imagined) with an activation of those cortical motor circuits that are responsible for the *execution* of that same action, without it resulting in an overt execution of the action. The motor activity, as it were, mimics, or mirrors, the perceived (or imagined) action. How the 'matching' between observed and executed actions comes about remains to be elucidated, but associative learning processes are likely to be involved. Some even argue that the 'mirroring' is caused entirely by associative learning processes, starting from a very early age, since the baby/infant tends to look at their own actions, for example to guide their actions to a desired goal (Heyes, 2010). According to the latter view, the functional significance of the mirroring process may be limited, as it is seen as merely a by-product of associative learning. However, the 'accidental' forming of connections between matching visual and motor representations may in fact, rather than being a useless by-product, have far-reaching consequences. Furthermore, the contribution of associative learning processes does not exclude the possibility that brains are programmed to project visual descriptions of others' actions (perceived or imagined), represented in the superior temporal sulcus (STS; Jellema and Perrett, 2003a,b; Pitcher and Ungerleider, 2021), onto the brain substrate that generates the execution of that action (without there being any intention to execute the action). The STS indeed projects heavily onto the parietal areas of the MNM (e.g., Rizzolatti and Luppino, 2001; Rozzi et al., 2006). In addition, the inferior temporal lobule projects to parietal mirror areas conveying information about the identity of the agent/object involved in the action (Borra et al., 2008).

Crucial for the proposed role of the MNM in social intuition is that the internal 'mimicking' of the observed action automatically makes a wealth of information available to the observer. That is, the off-line 'execution' of the observed action activates, apart from the motor representation of the action, also a range of action-associated areas. When one executes a particular action, numerous action-associated aspects, such as the accompanying visceral states (Critchley and Harrison, 2013), the action's effect or outcome in terms of reward or punishment (Prinz, 1997), the somatosensory feedback, and the most likely subsequent action (Braukmann et al., 2017) and/or response by another individual (Hunnius and Bekkering, 2010), all occur close in time to the action execution, and therefore get linked to the action representation. Thus, the mere observation of an action will make these linked aspects instantly available to the observer, which helps to immediately 'understand' the action in terms of its direct consequences and affective significance. In this view, the 'mirroring' may subserve the immediate, automatic, understanding of other's bodily articulations 'from within' (Rizzolatti and Sinigaglia, 2013, 2023), on the basis of one's own motor repertoires, experiences and feelings. The term 'understanding from within' alludes to the experiential nature of the neural processes involved, in contrast to a deliberate, effortful, inferential understanding of others, which is usually indicated as explicit Theory of Mind. Thus, one could envisage the MNM as part of the neural substrate for social intuition, enabling the quick 'understanding' of others' actions and gestures, on the basis of merely observing them.

4.1 Neural basis of action anticipation

Another reason for suggesting that the MNM may be part of the neural substrate for social intuition is that there are strong indications that it is sensitive to others' upcoming actions – i.e. action anticipation – on the basis of contextual cues that signal that the action is forthcoming (Urgesi et al., 2006; Kilner et al., 2007; Southgate et al., 2009; Maranesi et al., 2014; Braukmann et al., 2017; Krol et al., 2020). As discussed above, the ability to automatically anticipate others' actions is a crucial component of social intuition. Its neural basis has been investigated, in particular, using EEG (Electroencephalography), due to its superior temporal resolution (anticipation effects may be short-lived, < 1 s; Maranesi et al., 2014). In particular, suppression of the power of the mu rhythm (8–13 Hz), which can be recorded over sensorimotor and parietal cortex, has been taken as an index for MNM activity (thus, the larger the suppression the larger the neural activation). The main reason for this latter assumption is that Mu power suppressions occur both during the execution and observation of actions (see Fox et al. (2016) and Hobson and Bishop (2016, 2017), for critical evaluations of the supposed Mu-MNM link). Initially, it was thought that the MNM activates exclusively *during* the course of observed actions (1-to-1 resonation), but evidence is now accumulating that it also activates during the anticipation of upcoming predictable actions (Umiltà et al., 2001; Urgesi et al., 2006; Kilner et al., 2007; Csibra, 2008; Southgate et al., 2009; Maranesi et al., 2014; Krol et al., 2020). Some studies reported anticipatory power suppressions in the Beta frequency range (13–25 Hz; e.g. Braukmann et al., 2017; Monroy et al., 2019), rather than in the alpha range. In Braukmann et al. (2017), participants were presented with transient actions (e.g., making a cup of tea) consisting of three distinct action steps increasing in predictability: whereas the goal of step one was ambiguous, the goal of step three was highly predictable. The main finding was that predictive motor system activation, as indexed by beta-band attenuation, increased with increased predictability, with strongest activation prior to the final, most predictable, step. Intriguingly, there are indications that the Mu anticipation effects are much stronger in response to real-world actions presented by a live actor (Krol et al., 2020), as compared to actions presented in videos (Krol and Jellema, 2022, 2023). It is yet unclear why that is the case, but possibly the observer's engagement with the observed action plays a role.

It remains to be explored whether individuals with impaired social intuition, such as those with ASC, show less anticipatory mu suppression. If so, then that would be another indication for the involvement of the MNM in social intuition. With respect to Mu suppression *during* the observation of actions there are conflicting findings, There are reports of significantly weakened Mu suppression in ASC (e.g., Bernier et al., 2007; Oberman et al., 2013; Dumas et al., 2014), but others reported no difference (e.g., Fan et al., 2010; Ward et al., 2021). Overall there seems to be a trend toward weaker Mu suppression in individuals with ASC compared to TD individuals. The variation can be due to various factors, such as participant age, heterogeneity of the ASC sample, small number of participants, use of intransient actions or static images, or the use of a separate, rather than a within-trial, baseline.

Action anticipation is intrinsically linked to the action-chain organization of motor cortex (Fogassi et al., 2005). Goal-directed actions typically can be delineated as a sequence of discrete sub-actions, and each of these sequences is engrained in motor cortex in a unique manner (Fogassi et al., 2005). This means that neurons coding for say grasping an object to bring it to the mouth are different ones from neurons encoding an identical grasping action, but forming part of another action-chain, such as grasping the object to place it away. This seems an uneconomical way to represent action-chains in motor cortex, but it means that the entire action-chain can be triggered almost instantaneously, allowing the observer a peek into the future and a sense of the action's goal. Thus, the observer does not need to perform any deliberate, effortful thinking to figure out the next stage of the action, but just 'sees' it, as is typical for social intuition. Disruption of the automatic unfolding of action-chains might underpin impairments in reading the goal of others' actions. Cattaneo et al. (2007) showed, using electromyography recordings, that in children with ASC the automatic unfolding of action-chains indeed seems to be compromised.

Though EEG is well able to capture the relatively fast (< 1 s) anticipation effects, it lacks the spatial resolution to delineate the sensorimotor, parietal and occipital sources of the power suppressions in the 8-13 Hz frequency band. Therefore, fNIRS (functional near-infrared spectroscopy; Chiarelli et al., 2017), which depends on the relatively "sluggish" BOLD (blood oxygen level dependent) response, but offers good spatial resolution, in combination with EEG would be a way forward. Like EEG, but unlike fMRI, fNIRS allows real-world live action presentations, which seem a prerequisite to evoke Mu anticipation effects.

Recent studies suggest that anticipatory MNM activity can be triggered not only by explicitly learned information (such as a specific color signal, indicating that an action is upcoming, Krol et al., 2020), but, crucially, also by implicitly learned information (e.g., Braukmann et al., 2017; Monroy et al., 2019). This is highly relevant as it further supports the candidacy of the MNM as neural substrate for social intuition, since, as we argued, implicitly learned information forms the backbone of social intuition. In Monroy et al. (2019), in the acquisition phase, infants were shown videos displaying a hand performing six different actions uniquely directed at six different toys. Trials consisted either of deterministic action pairs (e.g., action A was always followed, after a 1 s delay, by action B) or of random pairs (e.g., action C was followed, after the 1 s delay, by any of the other five actions). In the test phase, the authors found that motor activity during the 1 s delay interval selectively increased in anticipation of deterministic actions and not prior to random actions. Given their mean age of 18 months, their learning might be classed as implicit learning.

We see the MNM as an important hub in the neural network supporting social intuition. This network likely includes various social brain areas (Frith, 2007; Adolphs, 2009; Yang et al., 2015), but, crucially, also areas involved in implicit learning, possibly including the caudate and putamen in the basal ganglia (Lieberman, 2000), and areas representing reward and feelings, such as the ventral striatum (e.g., Sims et al., 2014), amygdala (e.g., Stanley et al., 2008) and anterior insular cortex (e.g., Lamm and Singer, 2010).

5 Concluding remarks

The traditional non-social implicit learning paradigms, as implemented in for example the SRT and AGL tasks, do not allow to draw conclusions about the role of implicit learning processes in social intuition, as they lack a number of vital characteristics associated with social intuition, such as bodily articulations, affective valences and attitudes/dispositions. The premise put forward in this article is that social intuition is largely based on the implicit learning of associations between the other's bodily articulations and the consequences or outcomes in terms of subsequent actions and events, and associated affective valences. This means that: (i) the underlying structures of the learning processes may be relatively simple, and may not resemble the very complex structures that underpin the traditional tasks. (ii) Learning processes should be agile and relatively rapid, and should not require many hundreds of trials as in the traditional tasks. (iii) Affective valences should be incorporated in the paradigm, as these are a defining characteristic of social intuition (Cleeremans, 2011).

Attempts to 'socialise' the traditional AGL task have recently been undertaken (e.g., Jurchis et al., 2023; Jurchiş and Dienes, 2023), but these paradigms are still rather non-ecologically-valid and do not incorporate affective valences. The studies by Macinska and Jellema, highlighted in this article, are another attempt to address this issue. In this paradigm positive or negative valences are unconsciously associated with a particular identity, on the basis of implicitly learned contingencies between bodily articulations performed by that identity. This approach seems able to discriminate between individuals low and high in autistic traits. Whether an impairment in implicit affective learning in ASC, as suggested by these studies, indeed has consequences for the development of their social intuition skills remains to be confirmed. It should be noted, however, that while the Macinska and Jellema paradigm is more ecologically valid than other paradigms, it is still not really reminiscent of a social *interaction*. Further, a risk associated with the latter paradigm is that other forms of learning, such as perceptual learning, could possibly interfere with the results.

The cues on which implicit social learning is based consist, to a large extent, of bodily articulations (gestures, actions, facial expressions, eye gaze direction, vocalizations), all of which are specifically represented in the MNM. A major premise of this article is that the MNM is a crucial hub in the neural social intuition network. This, however, poses an interesting problem. According to the extensive literature on the MNM (e.g., Rizzolatti and Craighero, 2004), the main input to the MNM consists of the visual description of the other's action, which causes motor resonation in the MNM, leading to activation of associated areas that represent consequences of the observed action. These associated areas are those areas that would have been activated if the observer themselves would have carried out that action, and are therefore intricately linked to the action representation. Such consequences may consist of the most likely subsequent action/event, visceral states, affective states, sensory feedback and possible reward/punishment. This means that mere observation of the action makes these outcomes directly 'available' to the observer, and lead to what Rizzolatti and Sinigaglia (2013, 2023) called an 'experiential' understanding of the action (or understanding 'from within').

The interesting problem is that the 'immediate insight' we commonly call social intuition pertains to the other individual's attitude/disposition, not to the observer's own attitude/disposition; these two may differ profoundly. How then can motor resonation in the MNM bridge this gap? We propose that implicit social learning plays a crucial role. When the observation of the agent performing a particular action in a particular context does not trigger any implicitly learned information, then the observer's immediate social intuition regarding that agent will indeed be determined by their own repertoire of experiences (i.e., by what they would feel/do if they would carry out that action in that context). If, however, implicitly learned information is available and triggered, then that information will inform and dominate the observer's social intuition. The implicitly learned information may be linked to a particular individual, as in the paradigm presented in this article (note: identity information, originating in inferior temporal gyrus, is conveyed to the parietal MNM areas), or may be linked to individuals in general. The automatic use of information derived from implicit social learning may lead to accurate social intuition; without it an inaccurate, own-experience-centered, type of social intuition prevails. Possibly, social intuition in ASC individuals is too reliant on the latter pathway.

Implicit social learning also pertains to contextual cues that herald upcoming actions. In these cases, the cues themselves, rather than the observation of an action, trigger motor activity in the MNM. We argue that automatic action anticipation is a crucial contributor to social intuition, enabling the rapid judgments and responses made during fast-paced social interaction. The MNM provides a candidate neural substrate for such anticipatory representations of others' actions (e.g., Kilner et al., 2007; Krol et al., 2020). Importantly, anticipatory MNM activity can be triggered by implicitly learned information (e.g., Braukmann et al., 2017; Monroy et al., 2019). These findings need, however, be backed up by more research. Whether MNM activity in anticipation of others' actions is reduced in ASC remains to be clarified.

Finally, it should be noted that a limitation of the treatment of social intuition in this article is that it only deals with its automatic nature. For any human social intuition capacity to be meaningful in real-life social situations, higher-level knowledge and explicit, deliberate Theory-of-Mind (ToM) processes are required as well. Moreover, explicit ToM processes might interact with, or modulate, automatic processes (*cf.*, Wincenciak et al., 2022), such as social intuition. For example, one could speculate that when in our implicit social learning paradigm the participant *knows* that, even though they can see the agent, the agent cannot see them (because of one-way mirror), they might not implicitly learn to associate the agent with a positive or negative disposition toward them (even though the agent was looking right at them). MNM activation might also be sensitive to explicit ToM reasoning. For example, where observers might show anticipatory MNM activity when an agent's gaze is directed at a cup of coffee, which implicitly signals they are likely to grasp the cup and drink, they may not show this anticipatory MNM activity if they understood that the agent believed that the cup contained some other non-desired liquid. Such possible interactions between explicit ToM and automatic social intuition remain to be explored in future work.

Data availability statement

The datasets presented in this article are not readily available because they constitute preliminary data. Requests to access the datasets should be directed to T.Jellema@hull.ac.uk.

Ethics statement

The studies involving humans were approved by Ethics committee of the Faculty of Health Sciences of the University of Hull. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

TJ: Conceptualization, Writing – original draft. SM: Writing – review & editing. RO'C: Writing – review & editing. TS: Writing – review & editing.

Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annu. Rev. Psychol.* 60, 693–716. doi: 10.1146/annurev.psych.60.110707.163514

Aizenstein, H. J., Stenger, V. A., Cochran, J., Clark, K., Johnson, M., Nebes, R. D., et al. (2004). Regional brain activation during concurrent implicit and explicit sequence learning. *Cereb. Cortex* 14, 199–208. doi: 10.1093/cercor/bhg119

Amso, D., and Davidow, J. (2012). The development of implicit learning from infancy to adulthood: item frequencies, relations, and cognitive flexibility. *Dev. Psychobiol.* 54, 664–673. doi: 10.1002/dev.20587

Bargh, J. A. (1994). "The four horsemen of automaticity: awareness, intention, efficiency, and control in social cognition" in *Handbook of social cognition*. eds. R. S. Wyer and T. K. Srull, vol. *1* (Hillsdale, NJ: Erlbaum), 1–40.

Barnes, K. A., Howard, J. H., Howard, D. V., Gilotty, L., Kenworthy, L., Gaillard, W. D., et al. (2008). Intact implicit learning of spatial context and temporal sequences in childhood autism spectrum disorder. *Neuropsychology* 22, 563–570. doi: 10.1037/0894-4105.22.5.563

Baron-Cohen, S., Wheelwright, S., Skinner, S., Martin, J., and Clubley, E. (2001). The autism Spectrum quotient (AQ): evidence from Asperger syndrome/high functioning autism, males and females, scientists and mathematicians. *J. Autism Dev. Disord.* 31, 5–17. doi: 10.1023/A:1005653411471

Bayliss, A. P., and Tipper, S. P. (2006). Predictive gaze cues and personality judgments. *Psychol. Sci.* 17, 514–520. doi: 10.1111/j.1467-9280.2006.01737.x

Bechara, A., Damasio, H., Tranel, D., and Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science* 275, 1293–1295. doi: 10.1126/science.275.5304.1293

Bernier, R., Dawson, G., Webb, S., and Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain Cogn.* 64, 228–237. doi: 10.1016/j.bandc.2007.03.004

Borra, E., Belmalih, A., Calzavara, R., Gerbella, M., Murata, A., Rozzi, S., et al. (2008). Cortical connections of the macaque anterior intraparietal (AIP) area. *Cereb. Cortex* 18, 1094–1111. doi: 10.1093/cercor/bhm146

Braukmann, R., Bekkering, H., Hidding, M., Edita Poljac, E., Buitelaar, J. K., and Hunnius, S. (2017). Predictability of action sub-steps modulates motor system activation during the observation of goal-directed actions. *Neuropsychologia* 103, 44–53. doi: 10.1016/j.neuropsychologia.2017.07.009

Brown, J., Aczel, B., Jiménez, L., Kaufman, S. B., and Grant, K. P. (2010). Intact implicit learning in autism spectrum conditions. *Q. J. Exp. Psychol.* 63, 1789–1812. doi: 10.1080/17470210903536910

Burnett, H. G., and Jellema, T. (2013). (re-)conceptualisation in Asperger's syndrome and typical individuals with varying degrees of autistic-like traits. *J. Autism Dev. Disord.* 43, 211–223. doi: 10.1007/s10803-012-1567-z

Cattaneo, L., Fabbri-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., et al. (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proc. Natl. Acad. Sci. U S A* 104, 17825–17830. doi: 10.1073/pnas.0706273104

Chevallier, C., Kohls, G., Troiani, V., Brodkin, E. S., and Schultz, R. T. (2012). The social motivation theory of autism. *Trends Cogn. Sci.* 16, 231–239. doi: 10.1016/j.tics.2012.02.007

Chiarelli, A. M., Zappasodi, F., Di Pompeo, F., and Merla, A. (2017). Simultaneous functional near-infrared spectroscopy and electroencephalography for monitoring of human brain activity and oxygenation: a review. *Neurophotonics* 4:041411. doi: 10.1117/1.NPh.4.4.041411

Cleeremans, A. (2011). The radical plasticity thesis: how the brain learns to be conscious. *Front. Psychol.* 2:86. doi: 10.3389/fpsyg.2011.00086

Costea, A. R., Jurchiş, R., Visu-Petra, L., and Cleeremans, A. (2023). Implicit and explicit learning of socio-emotional information in a dynamic interaction with a virtual avatar. *Psychol. Res.* 87, 1057–1074. doi: 10.1007/s00426-022-01709-4

Critchley, H. D., and Harrison, N. E. (2013). Visceral influences on brain and behavior. *Neuron* 77, 624–638. doi: 10.1016/j.neuron.2013.02.008

Csibra, G. (2008). Action mirroring and action understanding: an alternative account. Sensorymotor foundations of higher cognition. *Attention Performance* XXII, 435–459. doi: 10.1093/acprof:oso/9780199231447.003.0020

Damasio, A. R. (1994). *Descartes' error: Emotion, reason, and the human brain*. New York: G.P. Putnam's Sons.

Dawson, G., Webb, S. J., and McPartland, J. (2005). Understanding the nature of face processing impairment in autism: insights from behavioral and electrophysiological studies. *Dev. Neuropsychol.* 27, 403–424. doi: 10.1207/s15326942dn2703_6

De Houwer, J., and Moors, A. (2012). "How to define and examine implicit processes?" in *Implicit and explicit processes in the psychology of science*. eds. R. Proctor and J. Capaldi (New York: OUP USA), 183–198.

Dienes, Z., and Scott, R. (2005). Measuring unconscious knowledge: distinguishing structural knowledge and judgment knowledge. *Psychol. Res.* 69, 338–351. doi: 10.1007/s00426-004-0208-3

DSM-V-TR (2022). *Diagnostic and statistical manual of mental disorders (5th ed., text revision)*. Washington, DC: American Psychiatric Publishing.

Dumas, G., Soussignan, R., Hugueville, L., Martinerie, J., and Nadel, J. (2014). Revisiting mu suppression in autism spectrum disorder. *Brain Res.* 1585, 108–119. doi: 10.1016/j.brainres.2014.08.035

Evans, J. B. T. (2003). In two minds. *Trends Cogn. Sci.* 7, 454–459. doi: 10.1016/j.tics.2003.08.012

Fan, Y. T., Decety, J., Yang, C. Y., Liu, J. L., and Cheng, Y. (2010). Unbroken mirror neurons in autism spectrum disorders: Unbroken mirror neurons in ASD. *J. Child Psychol. Psychiatry* 51, 981–988. doi: 10.1111/j.1469-7610.2010.02269.x

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667. doi: 10.1126/science.1106138

Foti, F., de Crescenzo, F., Vivanti, G., Menghini, D., and Vicari, S. (2015). Implicit learning in individuals with autism spectrum disorders: a meta-analysis. *Psychol. Med.* 45, 897–910. doi: 10.1017/S0033291714001950

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., et al. (2016). Assessing human mirror activity with EEG mu rhythm. *Psychol. Bull.* 142, 291–313. doi: 10.1037/bul0000031

Frith, C. D. (2007). The social brain? *Philos. Trans. R. Soc. B* 362, 671–678. doi: 10.1098/rstb.2006.2003

Frith, C. D. (2008). Social cognition. *Philos. Trans. R. Soc. B* 363, 2033–2039. doi: 10.1098/rstb.2008.0005

Gómez, J.-C., Kersken, V. A., Ball, D. N., and Seed, A. M. (2017). Knowing without knowing. *Stud. Psychol.* 38, 37–62. doi: 10.1080/02109395.2016.1268389

Gordon, B., and Stark, S. (2007). Procedural learning of a visual sequence in individuals with autism. *Focus Autism Other Dev. Disabil.* 22, 14–22. doi: 10.1177/10883576070220010201

Greenwald, A., and Banaji, M. R. (1995). Implicit social cognition: attitudes, self-esteem, and stereotypes. *Psychol. Rev.* 102, 4–27. doi: 10.1037/0033-295X.102.1.4

Hertwig, R., and Hoffrage, U.The ABC Research group. *Simple heuristics in a social world* (2013). Oxford: OUP

Heyes, C. (2010). Where do mirror neurons come from? *Neurosci. Biobehav. Rev.* 34, 575–583. doi: 10.1016/j.neubiorev.2009.11.007

Hobson, H. M., and Bishop, D. V. M. (2016). Mu suppression – a good measure of the human mirror neuron system? *Cortex* 82, 290–310. doi: 10.1016/j.cortex.2016.03.019

Hobson, H. M., and Bishop, D. V. M. (2017). The interpretation of mu suppression as an index of mirror neuron activity: past, present and future. *R. Soc. Open Sci.* 4:160662. doi: 10.1098/rsos.160662

Hudson, M., Burnett, H. G., and Jellema, T. (2012a). Anticipation of action intentions in autism Spectrum disorder. *J. Autism Dev. Disord.* 42, 1684–1693. doi: 10.1007/s10803-011-1410-y

Hudson, M., Liu, C. H., and Jellema, T. (2009). Anticipating intentional actions: the effect of eye gaze direction on the judgment of head rotation. *Cognition* 112, 423–434. doi: 10.1016/j.cognition.2009.06.011

Hudson, M., Nijboer, T. C. W., and Jellema, T. (2012b). Implicit social learning in relation to autistic-like traits. *J. Autism Dev. Disord.* 42, 2534–2545. doi: 10.1007/s10803-012-1510-3

Hunnius, S., and Bekkering, H. (2010). The early development of object knowledge: a study of infants' visual anticipations during action observation. *Dev. Psychol.* 46, 446–454. doi: 10.1037/a0016543

Jellema, T., Baker, C. I., Wicker, B., and Perrett, D. I. (2000). Neural representation for the perception of the intentionality of actions. *Brain Cogn.* 44, 280–302. doi: 10.1006/brcg.2000.1231

Jellema, T., Lorteije, J. A. M., van Rijn, S., van t' Wout, M., de Haan, E., van Engeland, H., et al. (2009). Involuntary interpretation of social cues is compromised in autism spectrum disorders. *Autism Res.* 2, 192–204. doi: 10.1002/aur.83

Jellema, T., Pecchinenda, A., Palumbo, L., and Tan, E. G. (2011). Biases in the perception and affective valence of neutral facial expressions induced by the immediate perceptual history. *Vis. Cogn.* 19, 616–634. doi: 10.1080/13506285.2011.569775

Jellema, T., and Perrett, D. I. (2003a). Cells in monkey STS responsive to articulated body motions and consequent static posture: a case of implied motion? *Neuropsychologia* 41, 1728–1737. doi: 10.1016/S0028-3932(03)00175-1

Jellema, T., and Perrett, D. I. (2003b). Perceptual history influences neural responses to face and body postures. *J. Cogn. Neurosci.* 15, 961–971. doi: 10.1162/089892903770007353

Jurchis, R., Costea, A., and Opre, A. (2023). A implicit and explicit learning of socio-emotional information are not related to the level of depressive symptomatology. *Motiv. Emot.* 47, 795–809. doi: 10.1007/s11031-023-10022-5

Jurchiş, R., and Dienes, Z. (2023). Implicit learning of regularities followed by realistic body movements in virtual reality. *Psychon. Bull. Rev.* 30, 269–279. doi: 10.3758/s13423-022-02175-0

Kahneman, D. (2011). *Thinking, Fast and Slow*. New York: Farrar, Straus and Giroux.

Kilner, J. M., Friston, K. J., and Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cogn. Process.* 8, 159–166. doi: 10.1007/s10339-007-0170-2

Kliemann, D., Rosenblau, G., Bölte, S., Heekeren, H. R., and Dziobek, I. (2013). Face puzzle – two new video-based tasks for measuring explicit and implicit aspects of facial emotion recognition. *Front. Psychol.* 4:376. doi: 10.3389/fpsyg.2013.00376

Krol, M. A., and Jellema, T. (2022). Sensorimotor anticipation of others' actions in real-world and video settings: modulation by level of engagement? *Soc. Neurosci.* 17, 293–304. doi: 10.1080/17470919.2022.2083229

Krol, M. A., and Jellema, T. (2023). Sensorimotor representation of observed dyadic actions with varying agent involvement: an EEG mu study. *Cogn. Neurosci.* 14, 25–35. doi: 10.1080/17588928.2022.2084605

Krol, M. A., Schutter, D. J. L. G., and Jellema, T. (2020). Sensorimotor cortex activation during anticipation of upcoming predictable but not unpredictable actions. *Soc. Neurosci.* 15, 214–226. doi: 10.1080/17470919.2019.1674688

Kunst-Wilson, W. R., and Zajonc, R. B. (1980). Affective discrimination of stimuli that cannot be recognized. *Science* 207, 557–558. doi: 10.1126/science.7352271

Lamm, C., and Singer, T. (2010). The role of anterior insular cortex in social emotions. *Brain Struct. Funct.* 214, 579–591. doi: 10.1007/s00429-010-0251-3

Lawrence, K. E., Hernandez, L. M., Eilbott, J., Jack, A., Aylward, E., Gaab, N., et al. (2020). Neural responsivity to social rewards in autistic female youth. *Psychiatry* 10. doi: 10.1038/s41398-020-0824-8

Lieberman, M. D. (2000). Intuition: A social cognitive neuroscience approach. *Psychol. Bull.* 126, 109–137. doi: 10.1037/0033-2909.126.1.109

Macinska, S. M. (2019). *Implicit social cognition in autism spectrum disorder. PhD Thesis*. Hull: University of Hull, UK.

Macinska, S. M., and Jellema, T. (2016). Implicit learning of social and non-social information. Conference paper presented at fifth implicit learning seminar, Lancaster, England.

Macinska, S. M., and Jellema, T. (2022). Memory for facial expressions on the autism Spectrum: the influence of gaze direction and type of expression. *Autism Res.* 15, 870–880. doi: 10.1002/aur.2682

Macinska, S. M., Krol, M., and Jellema, T. (2015a). Variations in implicit social learning in the typically-developed population. *Perception* 44:45.

Macinska, S. M., Krol, M, and Jellema, T (2015b). The capacity for implicit social learning in relation to autistic traits. Conference presentation: EuroAsianPacific joint conference on cognitive science, Turin, Italy.

Macinska, S. M., Lindsay, S., and Jellema, T. (2023). Visual attention to dynamic emotional faces in adults on the autism spectrum. *J. Autism Dev. Disord.* doi: 10.1007/s10803-023-05979-8

Maranesi, M., Livi, A., Fogassi, L., Rizzolatti, G., and Bonini, L. (2014). Mirror neuron activation prior to action observation in a predictable context. *J. Neurosci.* 34, 14827–14832. doi: 10.1523/JNEUROSCI.2705-14.2014

Monroy, C. D., Gerson, S. A., Domínguez-Martínez, E., Kaduk, K., Hunnius, S., and Reid, V. (2019). Sensitivity to structure in action sequences: an infant event-related potential study. *Neuropsychologia* 126, 92–101. doi: 10.1016/j.neuropsychologia.2017.05.007

Moors, A., and De Houwer, J. (2006). Automaticity: a conceptual and theoretical analysis. *Psychol. Bull.* 132, 297–326. doi: 10.1037/0033-2909.132.2.297

Nemeth, D., Janacsek, K., Balogh, V., Londe, Z., Mingesz, R., Fazekas, M., et al. (2010). Learning in autism: implicitly superb. *PLoS One* 5:e11731. doi: 10.1371/journal.pone.0011731

Nissen, M. J., and Bullemer, P. (1987). Attentional requirements of learning. *Cogn. Psychol.* 19, 1–32. doi: 10.1016/0010-0285(87)90002-8

Norman, E., and Price, M. C. (2012). Social intuition as a form of implicit learning: sequences of body movements are learned less explicitly than letter sequences. *Adv. Cogn. Psychol.* 8, 121–131. doi: 10.5709/acp-0109-x

Oberman, L. M., McCleery, J. P., Hubbard, E. M., Bernier, R., Wiersema, J. R., Raymaekers, R., et al. (2013). Developmental changes in mu suppression to observed and executed actions in autism spectrum disorders. *Soc. Cogn. Affect. Neurosci.* 8, 300–304. doi: 10.1093/scan/nsr097

Palumbo, L., Burnett, H. G., and Jellema, T. (2015). Atypical emotional anticipation in high-functioning autism. *Mol. Autism.* 6:47. doi: 10.1186/s13229-015-0039-7

Palumbo, L., and Jellema, T. (2013). Beyond face value: does involuntary emotional anticipation shape the perception of facial expressions? *PLoS One* 8:e56003. doi: 10.1371/journal.pone.0056003

Panasiti, M. S., Puzzo, I., and Chakrabarti, B. (2015). Autistic traits moderate the impact of reward learning on social behaviour. *Autism Res.* 9, 471–479. doi: 10.1002/aur.1523

Pelphrey, K. A., Morris, J. P., McCarthy, G., and Labar, K. S. (2007). Perception of dynamic changes in facial affect and identity in autism. *Soc. Cogn. Affect. Neurosci.* 2, 140–149. doi: 10.1093/scan/nsm010

Pitcher, D., and Ungerleider, L. (2021). Evidence for a third visual pathway specialized for social perception. *Trends Cogn. Sci.* 25, 100–110. doi: 10.1016/j.tics.2020.11.006

Prinz, W. (1997). Perception and action planning. *Eur. J. Cogn. Psychol.* 9, 129–154. doi: 10.1080/713752551

Rauch, S. L., Whalen, P. J., Savage, C. R., Curran, T., Kendrick, A., Brown, H. D., et al. (1997). Striatal recruitment during an implicit sequence learning task as measured by functional magnetic resonance imaging. *Hum. Brain Mapp.* 5, 124–132. doi: 10.1002/(SICI)1097-0193(1997)5:2<124::AID-HBM6>3.0.CO;2-5

Reber, A. S. (1967). Implicit learning of artificial grammars. *J. Verbal Learn. Verbal Behav.* 6, 855–863. doi: 10.1016/S0022-5371(67)80149-X

Reber, A. S. (1989). Implicit learning and tacit knowledge. *J. Exp. Psychol. Gen.* 118, 219–235. doi: 10.1037/0096-3445.118.3.219

Redcay, E., and Schilbach, L. (2019). Using second-person neuroscience to elucidate the mechanisms of social interaction. *Nat. Rev. Neurosci.* 20, 495–505. doi: 10.1038/s41583-019-0179-4

Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. Annual review. *Neuroscience* 27, 169–192. doi: 10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., and Luppino, G. (2001). The cortical motor system. *Neuron* 31, 889–901. doi: 10.1016/S0896-6273(01)00423-8

Rizzolatti, G., and Sinigaglia, C. (2013). "Understanding action from the inside" in *Action science: Foundations of an emerging discipline*. eds. W. Prinz, M. Beisert and A. Herwig (Cambridge, MA: MIT Press)

Rizzolatti, G., and Sinigaglia, C. (2023). *Mirroring brains: How we understand others from the inside*. Oxford: Oxford University Press.

Rozzi, S., Calzavara, R., Belmalih, A., Borra, E., Gregoriou, G. G., Matelli, M., et al. (2006). Cortical connections of the inferior parietal cortical convexity of the macaque monkey. *Cereb. Cortex* 16, 1389–1417. doi: 10.1093/cercor/bhj076

Sato, W., Krumhuber, E. G., Jellema, T., and Williams, J. H. G. (2019). Editorial: dynamic emotional communication. *Front. Psychol.* 10:2836. doi: 10.3389/fpsyg.2019.02836

Schilbach, L., Eickhoff, S. B., Cieslik, E. C., Kuzmanovic, B., and Vogeley, K. (2012). Shall we do this together? Social gaze influences action control in a comparison group, but not in individuals with high-functioning autism. *Autism* 16, 151–162. doi: 10.1177/1362361311409258

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., et al. (2013). Toward a second-person neuroscience. *Behav. Brain Sci.* 36, 393–414. doi: 10.1017/S0140525X12000660

Senju, A., Southgate, V., White, S., and Frith, U. (2009). Mindblind eyes: an absence of spontaneous theory of mind in Asperger syndrome. *Science* 325, 883–885. doi: 10.1126/science.1176170

Shiffrin, R. M., and Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychol. Rev.* 84, 127–190. doi: 10.1037/0033-295X.84.2.127

Sims, T. B., Neufeld, J., Johnstone, T., and Chakrabarti, B. (2014). Autistic traits modulate frontostriatal connectivity during processing of rewarding faces. *Soc. Cogn. Affect. Neurosci.* 9, 2010–2016. doi: 10.1093/scan/nsu010

Southgate, V., Johnson, M. H., Osborne, T., and Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biol. Lett.* 5, 769–772. doi: 10.1098/rsbl.2009.0474

Stanley, D., Phelps, E., and Banaji, M. (2008). The Neural Basis of Implicit Attitudes. *Current Directions in Psychological Science*, 17, 164–170. doi: 10.1111/j.1467-8721.2008.00568.x

Travers, B. G., Powell, P. S., Mussey, J. L., Klinger, L. G., Crisler, M. E., and Klinger, M. R. (2013). Spatial and identity cues differentially affect implicit contextual cueing in adolescents and adults with autism spectrum disorder. *J. Autism Dev. Disord.* 43, 2393–2404. doi: 10.1007/s10803-013-1787-x

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing: a neurophysiological study. *Neuron* 31, 155–165. doi: 10.1016/S0896-6273(01)00337-3

Urgesi, C., Valentina, M., Matteo, C., and Aglioti, S. (2006). Mapping implied body actions in the human motor system. *J. Neurosci.* 26, 7942–7949. doi: 10.1523/JNEUROSCI.1289-06.2006

Wachowicz, B. (2020). "The neural basis of intuitive decision making" in *Advances in science, technology, higher education and Society in the Conceptual age: STHESCA*. ed. T. Marek (San Diego, CA: AHFE International, USA)

Ward, E. K., Braukmann, R., Weiland, R. F., Bekkering, H., Buitelaar, J. K., and Hunnius, S. (2021). Action predictability is reflected in beta power attenuation and predictive eye movements in adolescents with and without autism. *Neuropsychologia* 157:107859. doi: 10.1016/j.neuropsychologia.2021.107859

Wincenciak, J., Palumbo, L., Epihova, G., Barraclough, N. E., and Jellema, T. (2022). Are adaptation aftereffects for facial emotional expressions affected by prior knowledge about the emotion? *Cognit. Emot.* 36, 602–615. doi: 10.1080/02699931.2022.2031907

Yang, D. Y. J., Rosenblau, G., Keifer, C., and Pelphrey, K. A. (2015). An integrative neural model of social perception, action observation, and theory of mind. *Neurosci. Biobehav. Rev.* 51, 263–275. doi: 10.1016/j.neubiorev.2015.01.020

Zhang, Q., Li, L., Guo, X., Zheng, L., Wu, Y., and Zhou, C. (2020). Implicit learning of symmetry of human movement and gray matter density: evidence against pure domain general and pure domain specific theories of implicit learning. *Int. J. Psychophysiol.* 147, 60–71. doi: 10.1016/j.ijpsycho.2019.10.008

frontiers | Frontiers in Psychology

TYPE Original Research
PUBLISHED 06 May 2024
DOI 10.3389/fpsyg.2024.1287952

OPEN ACCESS

EDITED BY
Florin Dolcos,
University of Illinois at Urbana-Champaign,
United States

REVIEWED BY
Laura Alonso-Recio,
Autonomous University of Madrid, Spain
Sarah Gunnery,
New England College, United States

*CORRESPONDENCE
Yasmin Abo Foul
✉ yasmin.abofoul@mail.huji.ac.il

RECEIVED 03 September 2023
ACCEPTED 08 April 2024
PUBLISHED 06 May 2024

CITATION
Abo Foul Y, Arkadir D, Demikhovskaya A, Noyman Y, Linetsky E, Abu Snineh M, Aviezer H and Eitan R (2024) Perception of emotionally incongruent cues: evidence for overreliance on body vs. face expressions in Parkinson's disease.
Front. Psychol. 15:1287952.
doi: 10.3389/fpsyg.2024.1287952

Perception of emotionally incongruent cues: evidence for overreliance on body vs. face expressions in Parkinson's disease

Yasmin Abo Foul[1,2]*, David Arkadir[2], Anastasia Demikhovskaya[3], Yehuda Noyman[3], Eduard Linetsky[2], Muneer Abu Snineh[2], Hillel Aviezer[1] and Renana Eitan[2,3,4,5]

[1]Department of Psychology, Hebrew University of Jerusalem, Jerusalem, Israel, [2]Brain Division, Hadassah-Hebrew University Medical Center, Jerusalem, Israel, [3]Neuropsychiatry Unit, Jerusalem Mental Health Center, Hebrew University of Jerusalem, Jerusalem, Israel, [4]Department of Medical Neurobiology (Physiology), Institute for Medical Research Israel-Canada, Hebrew University-Hadassah Medical School, Jerusalem, Israel, [5]Department of Psychiatry, Brigham and Women's Hospital, Harvard Medical School, Boston, MA, United States

Individuals with Parkinson's disease (PD) may exhibit impaired emotion perception. However, research demonstrating this decline has been based almost entirely on the recognition of isolated emotional cues. In real life, emotional cues such as expressive faces are typically encountered alongside expressive bodies. The current study investigated emotion perception in individuals with PD ($n = 37$) using emotionally incongruent composite displays of facial and body expressions, as well as isolated face and body expressions, and congruent composite displays as a baseline. In addition to a group of healthy controls (HC) ($n = 50$), we also included control individuals with schizophrenia (SZ) ($n = 30$), who display, as in PD, similar motor symptomology and decreased emotion perception abilities. The results show that individuals with PD showed an increased tendency to categorize incongruent face-body combinations in line with the body emotion, whereas those with HC showed a tendency to classify them in line with the facial emotion. No consistent pattern for prioritizing the face or body was found in individuals with SZ. These results were not explained by the emotional recognition of the isolated cues, cognitive status, depression, or motor symptoms of individuals with PD and SZ. As real-life expressions may include inconsistent cues in the body and face, these findings may have implications for the way individuals with PD and SZ interpret the emotions of others.

KEYWORDS

emotional integration, Parkinson's disease, body language, context, schizophrenia, emotional perception

1 Introduction

Emotion perception, a vital skill for successful social interactions, may be affected by neurological disease, psychiatric disorders, or normal aging of the brain (Phillips et al., 2003; Hayes et al., 2020). Such is the case in PD, a neurodegenerative disorder caused by the breakdown and death of the dopamine-secreting neurons of the substantia nigra pars compacta (for a review, see Argaud et al., 2018).

The hallmark manifestation of PD involves motor symptoms such as muscular rigidity, bradykinesia (slowness of movement), tremor, and decreased facial expressivity known as "masked face" (hypomimia), which manifest in the early stages of PD (Gelb et al., 1999; Assogna et al., 2008). Individuals with PD may also display significant non-motor symptoms, such as cognitive decline (Hindle et al., 2014), psychiatric symptoms (Schneider et al., 2008), and difficulties in social interactions, among other systemic symptoms. These non-motor manifestations dramatically impact their quality of life (Bernal-Pacheco et al., 2012).

1.1 Emotion perception difficulties in PD

One important class of difficulties in PD involves a wide range of emotion perception deficits, appearing in the early stages of the disease and deteriorating with its progression (Lin et al., 2016). These latter symptoms include impaired production and perception of emotional prosody (Schröder et al., 2010), impaired discrimination of affective speech (Pell and Leonard, 2003), as well as impaired production and perception of facial expressions (for a meta-analysis, see Jacobs et al., 1995; Simons et al., 2004; Gray and Tickle-Degnen, 2010; Gunnery et al., 2016). Recent meta-analyses and reviews have shown that individuals with PD have a generalized deficit in emotion perception across modalities, which is more pronounced for negative emotional expressions, specifically anger, fear, sadness, and disgust (Argaud et al., 2018; Coundouris et al., 2019; Gothwal et al., 2022). While these overall findings are important, specific results differ across studies, perhaps due to significant variance with regard to participants' characteristics (e.g., the PD stage, cognitive abilities) and experimental tasks and design. As part of this variance, Argaud et al. (2018) noted that roughly a third of the studies found no difference in facial expression perception between individuals with PD and controls.

1.2 Suggested underlying mechanism

The specific mechanisms underlying these difficulties in PD are still unclear. Emotion perception difficulties in PD are only partially accounted for by mood disorders, cognitive decline, disease severity, and dopamine replacement therapy (Argaud et al., 2018; Coundouris et al., 2019). Theories of *emotional embodiment* suggest that individuals decode facial expressions by partially simulating what they perceive via their own musculature, thus creating motoric re-experiencing of the relevant emotions in the self (Niedenthal, 2007). Such re-experiencing, known as sensorimotor simulation, was supported by several studies (Niedenthal, 2007; Winkielman et al., 2008; Wood et al., 2016). It was suggested that hypomimia (reduction in facial expression activity in PD) disturbs facial simulation feedback, a proposed process for recognizing emotional expressions according to theories of emotional embodiment (Gray and Tickle-Degnen, 2010; Péron et al., 2014; Argaud et al., 2018).

1.3 Considering context: importance of body expressions in emotion perception

Prior research on emotion perception difficulties in PD largely relied on tasks using decontextualized facial expressions—that is, participants view faces in isolation. While methodologically convenient and widely popular in the neuroscience literature, this experimental approach fails to consider the fact that during most physical interactions, facial expressions are typically encountered in a rich context, not as isolated cues. Faces are perceived within a broader visual context, first and foremost the expressive body, which may be congruent or incongruent with the affective signal of the face (Abramson et al., 2017). However, the process of face-context integration in individuals with PD is poorly understood despite its potential importance (Aviezer et al., 2008, 2017). While several visual contextual factors may influence facial expression perception, body expressions constitute an immediate, intra-target source of relevant information (Wieser and Brosch, 2012). In healthy young adults, emotionally congruent body expressions appearing with the face may boost facial expression perception, while emotionally incongruent bodies may dramatically alter facial expression perception (Meeren et al., 2005; Aviezer et al., 2008, 2012; Israelashvili et al., 2019). This effect is further strengthened in the healthy aging brain, such that body expressions play a considerably larger role for older adults when perceiving face-body composites (Abo Foul et al., 2018). Specifically, healthy older adults are more influenced by incongruent body cues than their younger counterparts, emphasizing the contextual importance of bodies and how they are perceptually integrated with faces during emotion perception (Noh and Isaacowitz, 2013; Abo Foul et al., 2018).

1.4 Gap in research and rationale for investigation

To the best of our knowledge, the perception of composite face-body expressions in PD has not been previously investigated. This approach may be more revealing than investigating isolated cues for several reasons. First, the ecological validity of this approach bears a closer approximation to real-life social and emotion perception difficulties experienced in individuals with PD (Gunnery et al., 2016). Second, and more specifically for PD, understanding the effect of body expressions and their integrated perception of faces is essential in disorders that principally affect the body. PD produces motor symptoms in the body and face (e.g., bradykinesia and hypomimia, respectively), which can be considered a naturally occurring motor manipulation, allowing one to test the impact of impaired motor simulation feedback on emotion perception processes. Investigating the impact of motor simulation feedback deficits and their contribution to contextualized emotion perception may shed light on the underlying mechanisms of emotion perception in PD. Thus, as accumulating findings suggest different perception processing of emotions for integrated faces with bodies, investigating emotion perception from combined cues in individuals with PD is important, both clinically and theoretically. As previously emphasized, PD is a multifaceted disorder that impacts various systems, including motor, cognitive, and emotional functions, posing a challenge to attributing any singular deficit to a specific underlying mechanism. While comparing findings to healthy control groups is essential, it may not provide a comprehensive understanding. To address this complexity, we included an additional clinical control group comprising individuals with schizophrenia (SZ), a disorder that shares several intriguing parallels with PD.

1.5 Comparison with schizophrenia

SZ is a neuropsychiatric disorder characterized by a cluster of positive symptoms, such as hallucinations, delusions, and disorganization, as well as a cluster of negative symptoms, which include "affective flattening" (reduced emotional expressions), difficulties in emotional perception, impoverished speech, motivation, anhedonia, and decreased social interaction (for meta-analyses, see Chan et al., 2010; Kohler et al., 2010). While antipsychotic medications effectively manage positive symptoms, they can lead to Parkinsonian-like motor disturbances, encompassing bradykinesia, rigidity, and hypokinesia in facial and bodily expressions (Andreasen and Flaum, 1991; Słowiński et al., 2017; de la Mora et al., 2020). Accumulating research indicates that disruptions in dopamine neurotransmission along neural pathways play a role in the foundation of SZ (de la Mora et al., 2020; Sonnenschein et al., 2020). Individuals with SZ encounter a wide array of challenges related to emotion perception, including difficulties in recognizing emotional vocalizations (for a meta-analysis, see Gong et al., 2021), in addition to the well-documented disturbances in perceiving facial emotional expressions (for a meta-analysis, see Kohler et al., 2010), which may manifest in the early stages of the disorder (Kring and Elis, 2013). Importantly and similar to PD, individuals with SZ exhibit reduced abilities in conveying emotional facial expressions (for a review, see Trémeau, 2022).

1.6 Similarities and parallels between PD and SZ

PD and SZ can be viewed as two related dopamine disorders, marked by impaired and imbalanced dopamine neurotransmission (Meder et al., 2019; de la Mora et al., 2020). The presence of Parkinsonian-like movement disorders in SZ and schizophrenia-like psychosis in PD may suggest dysfunction within a shared network that encompasses the cortex, basal ganglia, thalamus, and cerebellum, while those are linked to emotion perception abilities (Pierce and Péron, 2020; Walther et al., 2020). Individuals with PD and SZ showed emotion perception difficulties, but the precise mechanism underlying these difficulties remains unclear. A comparison of PD and SZ, in addition to healthy controls, may therefore offer insights into specific and unique aspects of the emotion perception process from integrated cues in PD.

TABLE 1 **Sample characteristics and the screening tests (ACE, MMSE, FAB, MOCA, and BDI) by groups.**

	PD ($n = 37$)	SZ ($n = 30$)	HC ($n = 49$)
Age range	28–71	30–80	27–74
Mean age (±SD)	61.41 (8.8)	57.17 (19.29)	60.80 (8.70)
Gender: female (%)	11 (30%)	13 (43%)	13 (27%)
Education: average years (±SD)	14.49 (2.91)	13.20 (2.93)	15.96 (2.06)
ACE scores: average (±SD)	89.73 (3.49) ($n = 37$)	77.62 (12.80) ($n = 29$)	94.41 (3.53) ($n = 49$)
ACE range	80–95	56–96	88–99
MMSE (±SD)	28.65 (1.11)	27.21 (2.34)	28.61 (0.98)
FAB scores: average (±SD)	15.89 (1.93) ($n = 37$)	13.40 (3.78) ($n = 27$)	16.37 (1.35) ($n = 49$)
MOCA scores: average (±SD)	25.41 (2.19) ($n = 27$)	23.23 (4.45) ($n = 30$)	26.18 (2.18) ($n = 49$)
BDI average (±SD)	11.67 (7.36) ($n = 36$)	21.28 (16.53) ($n = 29$)	(4.26) ($n = 48$)

ACE, Addenbrooke's Cognitive Examination; MMSE, Mini-Mental State Examination; FAB, Frontal Assessment Battery; MOCA, Montreal Cognitive Assessment; BDI, Beck Depression Inventory.

1.7 The current investigation

This study examined emotion perception in individuals with Parkinson's disease (PD) using integrated facial and bodily expressions. The performance of the PD group was compared to that of the HC group, as well as that of a group of individuals with SZ. The advantage of the incongruent cue approach is that the responses to the stimuli directly highlight what source (face or body) was prioritized by the perceiver in their judgment. We adopted a more ecological approach in which participants are requested to categorize the emotion of the person while being free to base their judgment on any cue they deem relevant. In addition, we examined emotion perception from isolated cues as well as from congruent faces with bodies. This allowed us to establish a baseline for the recognition of each expressive cue alone and of congruent cues in conjunction. The two clinical groups were age-matched and evaluated not only for emotion perception but also for their motor symptoms using the Unified Parkinson's Disease Rating Scale (UPDRS; Fahn and Elton, 1987). Finally, we included tests of cognition, depression, and motor function to examine if emotion perception abilities are mediated by these domains.

2 Method

2.1 Participants

Individuals with PD ($N = 37$), individuals with SZ ($N = 30$), and matched healthy controls (HC, $N = 50$) comprised our study population (see Sample Characteristics, Table 1). An *a priori* power analysis was conducted using G*Power3 (Faul et al., 2007) for sample size estimation, using the effect size from a related study (Abo Foul et al., 2018). Considering an alpha of 0.05 and a power of 0.95, the projected sample size needed with this effect size is approximately 36 for the main hypothesis test. The inclusion criteria for PD were (1) idiopathic PD diagnosed by a neurologist, (2) the absence of active or untreated additional neuropsychiatric disorder or psychosis, and (3) Mini Mental State Examination (MMSE) scores above 25. The inclusion criteria for SZ were (1) psychiatric diagnoses according to the criteria of the *Diagnostic and Statistical Manual of Mental Disorders, 5th edition* (DSM-5; American Psychiatric Association, 2013), (2) the absence of active or untreated neurological conditions, and (3) MMSE scores above 25. For the HC group, the inclusion criteria were (1) the absence of active neurological or neuropsychiatric conditions and (2) MMSE scores above 25.

Individuals with PD were recruited from the Hadassah Medical Center's neuropsychiatric clinic in Jerusalem. These participants received neuropsychological assessment as candidates for deep brain stimulation (DBS) surgery. Individuals with SZ were recruited from the Kfar Shaul Mental Health Center, Jerusalem. Characteristics of the clinical groups are shown in Table 3. Older adults were recruited either via (a) social media advertisements or (b) an online Israeli participants' pool (https://www.panel4all.co.il/pages/home.html).

Only one HC participant was excluded due to uncompleted experiment tasks. All those taking part had normal or corrected-to-normal vision. The study was approved by the Hebrew University of Jerusalem Ethics Committee and the IRB Committees of the Hadassah Medical Organization and Kfar Shaul Mental Health Center.

2.2 Stimuli: emotional expressions

Face-body composites were constructed with stimuli obtained from standardized sets. Stereotypical images of facial expressions of sadness, anger, fear, and happiness were taken from the Amsterdam Dynamic Facial Expression Set (ADFES) (van der Schalk et al., 2011). Stereotypical body expressions of sadness, anger, fear, and happiness were taken from the Bochum Emotional Stimulus Set (BESST) (Thoma et al., 2013). Six exemplars were used for each emotion, with equal representation across genders. Using Adobe Photoshop, we created realistically proportioned face-body composites by crossing all emotional categories of faces with bodies (Figure 1), resulting in combinations that were congruent (e.g., an angry face on an angry body) and incongruent (for example, an angry face on a fearful body). The experiment comprised three blocks, namely, (1) *body only*, (2) *face only*, and (3) *face with body*. The body-only and face-only blocks each contained 24 stimuli—six exemplars for each emotion (sadness, anger, fear, and happiness) from the sets indicated. The face-only block included isolated faces without bodies. The body-only block included bodies with blurred faces. The face-with-body block included 32 composite stimuli: eight congruent and 24 incongruent. These stimuli have been recently validated in a normal population (Lecker et al., 2017) and in healthy older adults (Abo Foul et al., 2018).

FIGURE 1
Examples of composite stimuli used in the experiment. **(A)** An example of a congruent stimulus—a fearful face combined with a fearful body. **(B)** An example of an incongruent stimulus—a happy face combined with an angry body. Reproduced with permission from the Bochum Emotional Stimulus Set (BESST) (Thoma et al., 2013) and Amsterdam Dynamic Facial Expression Set (ADFES) (van der Schalk et al., 2011).

2.3 Cognitive assessment

2.3.1 Addenbrookes' cognitive examination

ACE (Mioshi et al., 2006) is a paper-based test used for cognitive screening, characterized by good specificity and sensitivity for diagnosing different types of dementia (Mioshi et al., 2006). This test expands the Mini-Mental State Examination (MMSE) for diagnosing dementia. It examines six cognitive domains: orientation (10 points), attention (8 points), memory (35 points), verbal fluency (14 points), language (28 points), and visuospatial abilities (5 points), with a maximal score of 100. Validated versions in Hebrew (Newman, 2005), Arabic (Al Salman, 2013), and English (Mioshi et al., 2006) were used in the study, according to the native language of the participants. The internal consistency of ACE is high (Cronbach's coefficient $\alpha = 0.87$), and its test-retest reliability as evaluated by the intraclass correlation coefficient (ICC) ranges from 0.64 to 0.82 (Takenoshita et al., 2019).

2.3.2 Frontal assessment battery

FAB (Dubois et al., 2000) is a neuropsychological test designed to assess executive function and address dysexecutive syndrome. This 10-min test contains six domains, namely, conceptualization, mental flexibility, motor programming, sensitivity to interference, inhibitory control, and environmental autonomy. The maximum score is 18, with lower scores indicating greater impairments. The internal consistency of FAB as measured by Cronbach's coefficient α is 0.61 (Goh et al., 2019).

2.3.3 Montreal Cognitive Test

MOCA (Lifshitz et al., 2012) is a widely used 10-min cognitive screening test that comprises eight cognitive domains, namely, visuospatial perception, organizational skills, recognition, naming, short-term memory, attention, verbal ability, abstraction, and orientation. In this study, we used the Hebrew, Arabic, and English versions as they appear on the MoCA test website (www.mocatest.org). The internal consistency of MoCA is high (Cronbach's coefficient $\alpha = 0.89$), and its test-retest reliability as evaluated by ICC ranges from 0.64 to 0.82 (Bruijnen et al., 2020; Sala et al., 2020).

2.3.4 Beck depression inventory

BDI (Beck et al., 1996) is a widely used self-report questionnaire that measures the severity of depressive symptoms. We used validated versions in Hebrew (Gil and Gilbar, 2001), English (Beck et al., 1996), and Arabic (Abdel-Khalek, 1998), tailored to the native language of the participants. The questionnaire addresses different depression symptoms, scored on a scale of 0–3 [e.g., "(0) I don't feel sad" to "(3) I'm so sad or unhappy that I can't stand it"]. Higher total scores indicate more severe depressive symptoms. The internal consistency of BDI is high (Cronbach's coefficient $\alpha = 0.9$), and its test-retest reliability as evaluated by ICC ranges from 0.73 to 0.96 (Wang and Gorenstein, 2013).

2.4 Procedure

After providing consent, participants were assessed for cognitive state, followed by the emotion perception tests. The PD and SZ groups were assessed in person, and HC was tested online via Zoom to reduce the COVID-19 infection risk. A neurologist assessed individuals with PD and SZ for motor symptoms using the UPDRS (Fahn and Elton, 1987). At the time of testing, the PD and SZ groups were taking their regular dopaminergic and antipsychotic medications, respectively. Following cognitive assessment, participants performed the experimental emotion perception tasks. Patients were tested in person using an E-Prime-controlled computer, while healthy controls were tested using *Gorilla* (Anwyl-Irvine et al., 2019), an online experiment platform. Blocks (face, body, and face with body) and stimuli within each block were randomly ordered. Each stimulus appeared for 2,000 ms, but no time limit was imposed for responses. Participants were instructed to select the emotion that best reflected the target's feelings from a list of four labels, namely, fear, anger, sadness, and happiness. In the case of face-body composites, no instructions were given prioritizing the face or body; rather, responses were to be made based on the overall impression of the target's emotion. BDI was completed after the session.

2.5 Analysis strategy

2.5.1 Perception of emotion from incongruent composites

Because participants were not requested to base their answer on the face or the body, incongruent face–body composites do not yield an objective "accurate" response. Therefore, to quantify the recognition of emotion from incongruent composites, we analyzed the tendency to categorize the composites as conveying the emotion of the face, the body, or neither. This was done using a 3 (groups: PD, HC, and SZ) × 3 (categorization tendencies: as face, as body, and other) mixed ANOVA. As recent meta-analyses do not support substantial differences as a function of specific emotions (Coundouris et al., 2019), we pooled the main results across emotions. A detailed exploratory analysis of group differences broken down to specific facial emotional expressions is also provided in the Supplementary material.

2.5.2 Perception of faces, bodies, and congruent face-body composites

To assess affective perception, we calculated the mean perception accuracy of each participant separately for each emotion in each cue. As no specific *a priori* predictions were raised for differences in the perception of specific emotions, accuracy rates were pooled across emotions. The mean perception accuracy of each participant pooled across emotions was subjected to a 3 (groups: PD, HC, and SZ) × 3 (cues: isolated face, isolated body, and congruent faces with bodies) ANOVA. A detailed exploratory analysis with specific emotions is also provided in the Supplementary material using a 3 (groups: PD, HC, and SZ) × 3 (cues: isolated face, isolated body, and congruent face-body) × 4 (emotions: anger, sadness, fear, and happiness) mixed ANOVA.

2.5.3 Additional analysis

We also examined the correlations between affective perception accuracy, categorization tendency, cognitive screening test scores, BDI, years of education, and motor UPDRS scores. When required, p-values were adjusted using Greenhouse-Geisser correction, with Bonferroni corrections applied for follow-up t-tests.

3 Results

3.1 Demographic and clinical characteristics

The demographic, cognitive, and clinical characteristics of the experiment groups are shown in Tables 1–3. The groups were age-matched ($p = 0.33$) and, importantly, no differences were found between the clinical groups in the UPDRS motor score ($p = 0.66$). Predictably, the groups differed in cognitive performance: HC scored highest in ACE, followed by individuals with PD, while individuals with SZ scored lowest (all t-contrasts $p < 0.001$). The PD and HC groups showed comparable cognitive performance in MMSE and FAB (both $p = 1$), whereas the SZ group was the lowest (all t-contrasts $p < 0.001$). Individuals with SZ scored highest for depression in the BDI, followed by those with PD, with HC reporting the lowest scores (all t-contrasts $p < 0.001$). The PD and SZ groups had comparable levels of education ($p = 0.14$), which were lower than those in the HC group (all t-contrasts $p < 0.01$).

TABLE 2 Summary of mixed analysis of variance (ANOVA) for age, years of education, and screening tests (ACE, MMSE, FAB, MOCA, and BDI).

	Df	*F*	*P*
Age	(2, 113)	1.13	0.33
Education years	(2, 113)	10.90	<0.001
MOCA	(2, 103)	9.13	<0.001
ACE	(2, 112)	51.72	<0.001
MMSE	(2, 112)	10.11	<0.001
FAB	(2, 113)	15.60	<0.001
BDI	(2, 110)	25.42	<0.001

ACE, Addenbrooke's Cognitive Examination; MMSE, Mini-Mental State Examination; FAB, Frontal Assessment Battery; MOCA, Montreal Cognitive Assessment; BDI, Beck Depression Inventory.

3.2 Perception of emotionally incongruent faces with bodies in PD, SZ, and HC

A 3 (groups: PD, SZ, and HC) × 3 (categorization tendencies: as face, as body, and as other) mixed ANOVA was performed on the categorizations (see Figure 2). Significant effects were found for categorization tendency, $F_{(2,226)} = 139.35$, $p < 0.001$, $\eta^2_p = 0.55$, and for the interaction of group × categorization tendency, $F_{(2,226)} = 5.64$, $p < 0.001$, $\eta^2_p = 0.09$. Follow-up comparisons revealed that individuals with PD were more likely to be affected by body cues than the HC ($p = 0.026$) and SZ groups ($p = 0.006$). HC had a greater tendency to categorize the composites according to facial expression than the PD group ($p = 0.006$) but no difference was found between the HC and SZ groups ($p = 0.64$). Individuals with SZ were more likely than HC ($p = 0.001$) and more likely than individuals with PD ($p = 0.03$) to categorize composites as conveying an emotion not presented in the face or body.

TABLE 3 Clinical characteristics of Individuals with PD and SZ.

	PD		SZ		
	n	Mean (SD)	*n*	Mean (SD)	*p*-value
Mean disease duration	37	11.62 (8.76)	27	27.19 (15.52)	<0.001
Dominance (right)	31 (83.78%)	27 (90%)			
LEDD (mg/day)	37	1,215.9 (565.1)			
UPDRS—mentation, behavior, and mood	26	3.23 (1.50)	30	4.20 (3.16)	0.16
UPDRS—ADL	26	10.88 (5.27)	30	4.70 (4.17)	< 0.001
UPDRS—"On" motor examination	35	19.09 (8.67)	30	20.10 (9.71)	0.66
UPDRS—"On" face	26	1.00 (0.57)	30	0.93 (0.64)	0.68
UPDRS—"On" total score	26	35.65 (12.87)	30	28.47 (14.21)	0.054
UPDRS—"Off" motor examination	35	40.31 (11.66)			
UPDRS—"Off" total score	27	62.41 (16.47)			
Native language (Hebrew)	26 (70.27%)	29 (96.67%)			
First motor symptom (for PD individuals)					
Right bodyside	15				
Left bodyside	17				
Slowness	3				
Walking disturbances	2				

PD, Parkinson's disease; SZ, individuals with schizophrenia; LEDD, levodopa equivalent daily dose; UPDRS, Unified Parkinson's Disease Rating Scale.

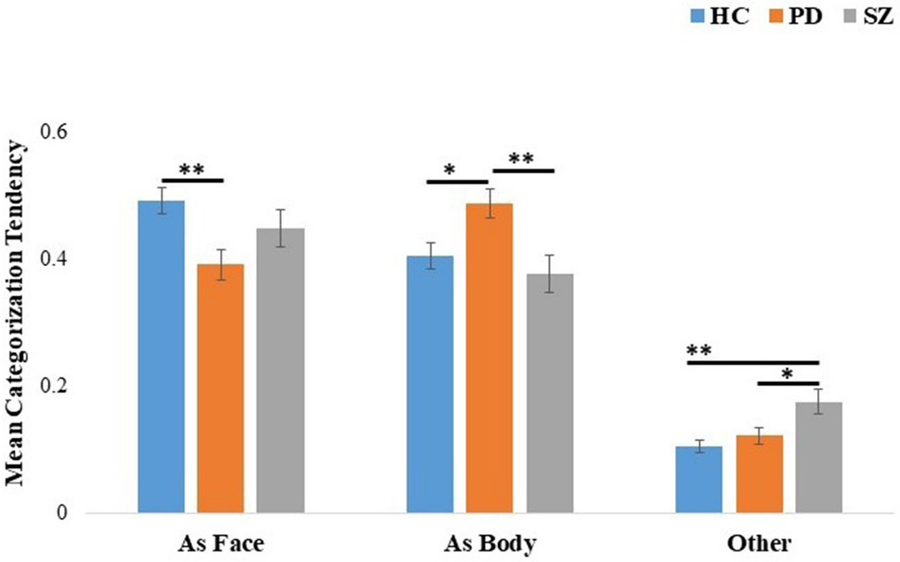


FIGURE 2
Mean categorization tendency of incongruent face-body composite stimuli for the HC, PD, and SZ groups. The categorization tendency [as face-emotion, body-emotion, and other (categorizations do not correspond to face or body emotions)] is shown on the *x*-axis. Error bars represent standard errors. *$p < 0.05$, **$p < 0.01$. HC, healthy controls; PD, Parkinson's disease group; SZ, schizophrenia group.

3.3 Group differences in emotion perception: isolated faces, isolated bodies, and emotionally congruent faces with bodies

A 3 (groups: PD, SZ, and HC) × 3 (cues: face, body, and face with body) mixed ANOVA was run on the mean affective perception accuracy per cue for each participant (see Figure 3). The results revealed significant effects for cue, $F_{(2,226)} = 12.05$, $p < 0.001$, $\eta^2_p = 0.10$, group, $F_{(2,113)} = 6.56$, $p = 0.002$, $\eta^2_p = 0.10$, and importantly for the cue × group interaction, $F_{(4,226)} = 2.54$, $p = 0.04$, $\eta^2_p = 0.04$. To interpret the interaction effects, comparisons between the experimental groups for each cue were performed. For isolated faces, the groups showed comparable mean affective perception accuracy ($p = 0.07$). For isolated bodies, the SZ group showed significantly worse recognition compared to both the PD and HC groups (both $ps = 0.001$), while the PD group did not differ from the HC group ($p = 0.9$). Finally, a trend was found in differences for the perception of emotionally congruent faces with bodies across groups ($p = 0.049$).

To strengthen our inferences concerning the lack of difference in comparing PD and HC groups in the perception of isolated cues, we conducted Bayesian comparisons. The corresponding Bayes factors suggested moderate evidence for the null hypothesis relative to the alternative hypothesis in the affective perception of isolated faces: $BF_{01} = 4.38$ and for isolated bodies: $BF_{01} = 4.144$.

3.4 Correlations between the categorization tendency of incongruent composites with cognitive screening tests, BDI, motor UPDRS, and education years

We next examined whether the categorization tendency in emotionally incongruent faces and bodies is related to participant performance in the cognitive tests, depression scores from the BDI questionnaire, motor state from the UPDRS score, and educational level by calculating Pearson's bivariate correlations. Full results are shown in Supplementary Table S2. No significant correlations were found in any of the groups between the tendency to categorize incongruent composites as face or body and participant performance in the cognitive tests (ACE, MoCA, and FAB), their averaged years of education, or their BDI scores. No significant correlations were found between the tendency to categorize as body or face and the motor UPDRS scores and UPDRS face scores of the clinical groups ($p > 0.1$).

3.5 Correlations between the mean affective perception accuracy of isolated faces, isolated bodies, and congruent faces with bodies with cognitive screening tests, BDI, motor UPDRS, and education years

To examine whether the mean affective perception of the isolated faces, isolated bodies, or congruent faces and bodies

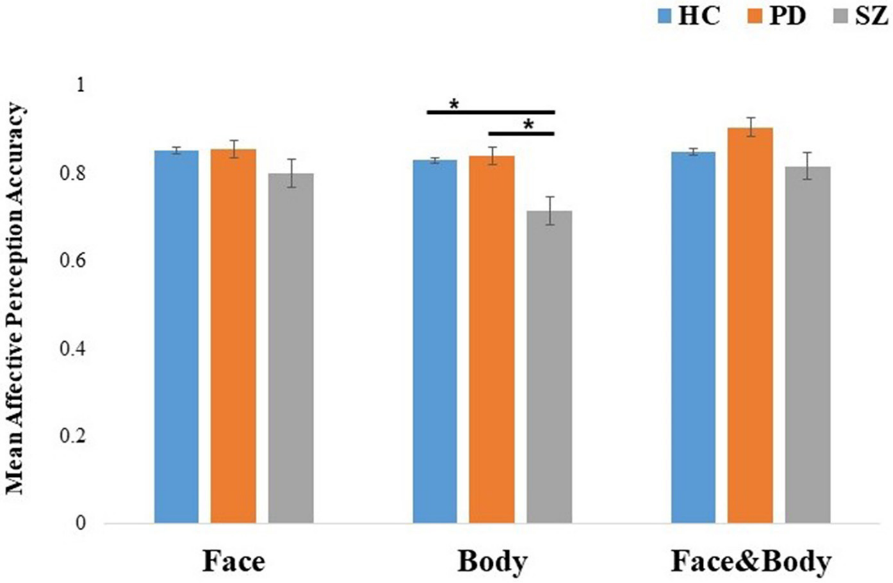


FIGURE 3
Mean effective perception accuracy of emotion recognition by cue: face, body, and congruent faces with bodies for HC, PD, and SZ. The results were pooled across emotions. Error bars represent standard errors. $*p < 0.001$. HC, healthy controls; PD, Parkinson's disease group; SZ, schizophrenia group.

is related to participants performance in cognitive screening, depression, motor UPDRS, and educational level, Pearson's bivariate correlations were calculated, see Supplementary Table S3 for full results. Results show that in the SZ group, higher cognitive performance, as tested by MOCA and ACE, was positively correlated with better emotion perception of the isolated body ($r = 0.43$ and $r = 0.43$, respectively) and isolated facial expressions ($r = 0.55$ and $r = 0.57$, respectively). Significant correlations were found between FAB scores and recognition of isolated facial ($r = 0.50$), body ($r = 0.43$), and congruent faces with bodies ($r = 0.42$) in the SZ group, indicating that higher scores in executive functions are positively correlated with the perception of all of the emotional cues. Additionally, a significant correlation was found between the UPDRS motor score and the mean perception of facial expressions ($r = -0.43$), but not with isolated bodily expressions or congruent faces with bodies.

In the PD group, significant positive correlations were found between the mean affective perception accuracy of isolated bodies and MOCA, $r = 0.41$, and FAB scores, $r = 0.44$. In the HC group, there were significant positive correlations between the mean affective perception accuracy of isolated bodies and MOCA scores, $r = 0.29$, and the mean affective perception accuracy of isolated faces and FAB scores, $r = 0.38$. Additionally, despite the lack of statistically significant findings, there were weak negative correlations (ranging from -0.25 to -0.31) observed between UPDRS facial scores and the average accuracy of emotional cue perception.

While not reaching statistical significance, it is noteworthy that a correlation emerged between ACE scores and the mean perception accuracy of emotional cues in both the HC and PD groups (r ranged from 0.23 to 0.31), suggesting a moderate effect size. Together with SZ group findings, the results suggested that individuals who performed worse at selecting the correct emotion in the face or body had lower cognition scores.

4 Discussion

The objective of this study was to examine emotion perception among individuals with PD by assessing their ability to integrate emotionally incongruent face-body composites as well as these cues presented individually and congruently. PD performance was compared to HC and, more importantly, to the SZ group. The results demonstrated that when incongruent face-body expressions were presented as composites, individuals with PD tended to categorize them based on the body's emotion, while HC predominantly categorized them according to the facial emotion. Notably, there was no consistent inclination toward prioritizing either the face or the body in the case of individuals with SZ. When faces and bodies were perceived in isolation, no significant differences emerged between PD and HC in our sample. In contrast, the SZ group showed significantly worse recognition of isolated bodies compared to both the PD and HC groups. When emotionally congruent faces with bodies were presented together, no significant differences were found between the research groups. Thus, the differences between individuals with PD, SZ, and HCs in prioritizing the body over the face could not be explained by the better accuracy or clarity of the isolated cues that formed the composite stimuli. Furthermore, no substantial correlations were identified between cognitive abilities, executive functions, and the categorization tendencies for incongruent composites observed in individuals with PD, SZ, and HC.

4.1 Exploring emotion perception abilities in PD and SZ

The reason for the comparable recognition of isolated faces in individuals with Parkinson's disease (PD) and healthy controls (HC) in our study remains unclear. While such findings are not rare in the literature—approximately one-third of studies indicate no differences in the perception of isolated facial expressions in PD—the typical results demonstrate poorer emotion recognition in PD compared to controls. One potential explanation could be linked to the specific characteristics of the PD individuals preselected as suitable candidates for Deep Brain Stimulation (DBS) procedures. According to DBS referral guidelines, these individuals have idiopathic PD without dementia and lack uncontrolled additional neuropsychiatric disorders (Silberstein et al., 2009). This unique subgroup of PD individuals might contribute to the observed comparable recognition of isolated facial expressions, suggesting that individuals selected for DBS may have a distinct profile or progression of PD impacting facial expression recognition. A second plausible explanation involves dopaminergic replacement therapy (DRT). DRT could influence the perception of facial expressions in two ways: (1) in the late stages of the disease, it may have a beneficial effect (Péron et al., 2014). (2) DRT activates the default mode network, enhancing attentional resources to external cues and emotion perception consequently (Delaveau et al., 2010). In the current investigation, individuals with PD were in the late stages of the disease and were examined while on their regular DRT.

Our results are in accordance with previous findings showing decreased emotion perception abilities in SZ. Individuals with SZ frequently face difficulties in accurately identifying and understanding emotional cues, leading to compromised social functioning and interpersonal difficulties. Kohler et al. (2010) meta-analysis revealed consistent impairments in facial emotion recognition among individuals with SZ, indicating a specific vulnerability in processing facial expressions. Green et al. (2015) further associated emotion perception deficits with poorer functional outcomes in schizophrenia, underscoring the clinical relevance of these impairments.

4.2 Exploring contextualized emotion perception in PD and SZ: insights from facial and body cues integration

Emotion perception abilities were widely investigated in various neuropsychiatric conditions, including SZ and PD, while those usually based on emotion perception of facial expressions were void of context. Recent studies stress the critical role of emotional context—specifically, emotional body context—in perceiving emotion. Information derived from body expression is utilized to disambiguate facial expressions (Aviezer et al., 2008, 2012, 2017). In healthy aging, older adults who perceive incongruent cues are more affected by body vs. face cues than young adults (Abo Foul et al., 2018). In this sense, a response pattern prioritizing body context over faces may reflect an adaptive compensatory approach, potentially beneficial in real-life conditions when a face may be more ambiguous than its context (Abramson et al., 2017; Israelashvili et al., 2019).

It is noteworthy that only a limited number of studies have explored PD individual's capacity to integrate information from multiple cues, whether unimodal or multimodal. For example, Fearon et al. (2015) demonstrated multi-modal facilitation in PD patients using congruent audiovisual stimuli. In our study, participants perceiving composite stimuli were not instructed to base their responses on the face or body but were encouraged to form an overall impression of the expressive target, mirroring daily social interactions. Furthermore, our sample of individuals with PD exhibited proficient perception of both facial and bodily cues when presented independently. These findings raise intriguing questions about the nature and implications of contextualized emotional expression perception in PD and its intricate interplay with other aspects of the disorder.

In the context of receiving multiple emotional cues, individuals with SZ face challenges in multi-sensory integration, as highlighted by Lin et al. (2020) review, suggesting difficulties at different stages of emotional processing. Reflecting on our results, individuals with SZ in the current study were worse at recognizing body emotions and exhibited no consistent pattern in integrating incongruent facial and bodily cues. Furthermore, when they showed incongruent face-body composites, they displayed a disproportionate level of responses that did not fit the face or the body. This response pattern was absent in SZ, suggesting emotion perception deficits may contribute to their social interaction difficulties. Altogether, these findings suggest a breakdown in emotion perception capabilities, especially when the target is complex and potentially ambiguous.

The distinct emotional perception patterns in PD and SZ, despite shared motor symptoms and affective flattening, may hint that motor symptomology alone cannot explain the observed differences. In our study, emotional perception patterns concerning incongruent cues did not correlate with the severity of motor symptoms in the face or the body in either the PD or SZ groups. In line with recent work (Vannuscorps et al., 2020), the current results challenge the hypothesized link between mimicry and emotion perception (Ricciardi et al., 2015, 2017), with embodiment theories positing that recognizing emotional states in others necessitates the simulation of the motor production of the perceived emotional expression, known as sensorimotor simulation (Wood et al., 2016).

In a comprehensive review of the integration of cues from the whole person, Hu et al. (2020) suggest two centers of face-body integration, namely, (1) the dorsal social agent hub that integrates face and body and other temporally synchronous cues and (2) the ventral semantic visual hub, which assimilates contextually semantic information. Although this model does not explicitly address emotion processing in the whole person, our findings, derived from comparisons between neuropsychiatric groups, may present preliminary evidence for the separate processing of emotion perception based on integrated facial and body cues. Exploring the utilization of whole-person cues could prove to be a valuable focus for future research, offering a naturalistic approach that contributes both theoretical and clinical insights to the study of emotion perception.

4.3 Limitations and future directions

Several limitations should be noted in the current work. First, although it included combined facial and body expressions, which are closer to what one encounters in real-life interactions, the stimuli were posed, stereotypical, and static emotional expressions. Recent findings stress the importance of investigating emotional perception using dynamic stimuli, especially in older adults (Abo Foul et al., 2022). Future research utilizing more ecologically oriented stimuli is needed. Second, despite attempts to ensure the matching of age among the experimental groups and of motor UPDRS scores among the clinical groups, differences in cognitive performance were noted. While these differences could potentially influence emotional perception abilities, we believe they are unlikely to account for our primary findings, as correlations with the cognitive scores were found in all of the experiment groups. Future research with larger samples is needed to explore the effects of cognitive abilities and other potential moderators on face-body emotion perception, such as gender. Third, the study focused exclusively on a single aspect of social perception—the perception of emotional visual stimuli. Future studies should broaden their scope to include a wider range of social perception aspects (Castro and Isaacowitz, 2019; Schlegel et al., 2020). Fourth, healthy controls were assessed online, whereas the clinical groups were evaluated in person. Although it remains unclear how such differences might contribute to the specific pattern of results observed, it is plausible that differences in testing methods might yield overall broader discrepancies in results. Consequently, further research conducted under similar experimental conditions is warranted.

Finally, additional exploration is warranted to better understand the relationship between facial motor symptoms and emotion perception. The present investigation may lack sensitivity in revealing connections between facial masking and emotion perception abilities for two main reasons. First, the sample size may be insufficiently powered to detect subtle differences, and second, the UPDRS assessment of facial motor symptoms is somewhat rudimentary and subjective. Future research examining the link between motor symptomatology and emotion perception could benefit from incorporating additional measures, such as electromyography (EMG) and automated video analysis, to assess muscle activity in facial expressions while also employing a larger sample size. This more comprehensive approach would provide valuable insights into the intricate interplay between facial motor function and the perception of emotions.

4.4 Caveats and conclusion

The current study found that individuals with PD showed an increased tendency to categorize incongruent face-body combinations in line with the body emotion, whereas those with HC showed a tendency to classify them in line with the facial emotion. Importantly, individuals with SZ showed no consistent pattern alongside responses that did not correspond to the face or body. These results were not explained by the recognition of the isolated face or body cues, cognitive status, depression, or motor symptoms. As real-life expressions may include inconsistent cues in the body and face, these findings may have implications for the way individuals with PD and SZ interpret the emotions of others.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving humans were approved by the Hebrew University of Jerusalem Ethics Committee and the IRB Committees of the Hadassah Medical Organization and Kfar Shaul Mental Health Center. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

YA: Formal analysis, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. DA: Writing – review & editing. AD: Writing – review & editing. YN: Writing – review & editing. EL: Writing – review & editing. MA: Writing – review & editing. HA: Conceptualization, Supervision, Writing – review & editing. RE: Conceptualization, Resources, Supervision, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was supported by Israel Science Foundation (ISF) grants to HA (#259/18) and RE (#1129/12 and #2128/19).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2024.1287952/full#supplementary-material

References

Abdel-Khalek, A. M. (1998). Death, anxiety, and depression in Lebanese undergraduates. *OMEGA-J. Death Dying* 37, 289–302. doi: 10.2190/CN5K-XF4C-2NPG-17E0

Abo Foul, Y., Eitan, R., and Aviezer, H. (2018). Perceiving emotionally incongruent cues from faces and bodies: older adults get the whole picture. *Psychol. Aging* 33:660. doi: 10.1037/pag0000255

Abo Foul, Y., Eitan, R., Mortillaro, M., and Aviezer, H. (2022). Perceiving dynamic emotions expressed simultaneously in the face and body minimizes perceptual differences between young and older adults. *J. Gerontol. Ser. B*, 77, 84–93. doi: 10.1093/geronb/gbab064

Abramson, L., Marom, I., Petranker, R., and Aviezer, H. (2017). Is fear in your head? A comparison of instructed and real-life expressions of emotion in the face and body. *Emotion* 17, 557–565. doi: 10.1037/emo0000252

Al Salman, A. S. A. (2013). *The Saudi Arabian adaptation of the Addenbrooke's Cognitive Examination–Revised (Arabic ACE-R)* (Doctoral dissertation). University of Glasgow.

American Psychiatric Association (2013). *Diagnostic and Statistical Manual of Mental Disorders, 5th Edn.* doi: 10.1176/appi.books.9780890425596

Andreasen, N. C., and Flaum, M. (1991). Schizophrenia: the characteristic symptoms. *Schizophr. Bull.* 17, 27–49. doi: 10.1093/schbul/17.1.27

Anwyl-Irvine, A. L., Massonié, J., Flitton, A., Kirkham, N. Z., and Evershed, J. K. (2019). Gorilla in our midst: an online behavioural experiment builder. *Behav. Res. Methods.* 52, 388–407. doi: 10.3758/s13428-019-01237-x

Argaud, S., Vérin, M., Sauleau, P., and Grandjean, D. (2018). Facial emotion recognition in Parkinson's disease: a review and new hypotheses. *Mov. Disord.* 33, 554–567. doi: 10.1002/mds.27305

Assogna, F., Pontieri, F. E., Caltagirone, C., and Spalletta, G. (2008). The recognition of facial emotion expressions in Parkinson's disease. *Eur. Neuropsychopharmacol.* 18, 835–848. doi: 10.1016/j.euroneuro.2008.07.004

Aviezer, H., Ensenberg, N., and Hassin, R. R. (2017). The inherently contextualized nature of facial emotion perception. *Curr. Opin. Psychol.* 17, 47–54. doi: 10.1016/j.copsyc.2017.06.006

Aviezer, H., Hassin, R. R., Ryan, J., Grady, C., Susskind, J., Anderson, A., et al. (2008). Angry, disgusted, or afraid? Studies on the malleability of emotion perception. *Psychol. Sci.* 19, 724–732. doi: 10.1111/j.1467-9280.2008.02148.x

Aviezer, H., Trope, Y., and Todorov, A. (2012). Body cues, not facial expressions, discriminate between intense positive and negative emotions. *Science* 338, 1225–1229. doi: 10.1126/science.1224313

Beck, A., Steer, R., and Brown, G. (1996). Beck depression inventory-II. *San Antonio* 78, 490–498. doi: 10.1037/t00742-000

Bernal-Pacheco, O., Limotai, N., Go, C. L., and Fernandez, H. H. (2012). Nonmotor manifestations in Parkinson disease. *Neurologist* 18, 1–16. doi: 10.1097/NRL.0b013e31823d7abb

Bruijnen, C. J. W. H., Dijkstra, B. A. G., Walvoort, S. J. W., Budy, M. J. J., Beurmanjer, H., De Jong, C. A. J., et al. (2020). Psychometric properties of the Montreal Cognitive Assessment (MoCA) in healthy participants aged 18-70. *Int. J. Psychiatry Clin. Pract.* 24, 293–300. doi: 10.1080/13651501.2020.1746348

Castro, V., and Isaacowitz, D. (2019). The same with age: Evidence for age-related similarities in interpersonal accuracy. *J. Exp. Psychol.* 148, 1517–1537. doi: 10.1037/xge0000540

Chan, R. C., Li, H., Cheung, E. F., and Gong, Q. Y. (2010). Impaired facial emotion perception in schizophrenia: a meta-analysis. *Psychiatry Res.* 178, 381–390. doi: 10.1016/j.psychres.2009.03.035

Coundouris, S., Adams, A., Grainger, S., and Henry, J. (2019). Social perceptual function in Parkinson's disease: a meta-analysis. *Neurosci. Biobehav. Rev.* 104, 255–267. doi: 10.1016/j.neubiorev.2019.07.011

de la Mora, M. P., Hernandez-Mondragon, C., Crespo-Ramirez, M., Rejon-Orantes, J., Borroto-Escuela, D. O., and Fuxe, K. (2020). Conventional and novel pharmacological approaches to treat dopamine-related disorders: focus on Parkinson's disease and schizophrenia. *Neuroscience* 439, 301–318. doi: 10.1016/j.neuroscience.2019.07.026

Delaveau, P., Salgado-Pineda, P., Fossati, P., Witjas, T., Azulay, J. P., and Blin, O. (2010). Dopaminergic modulation of the default mode network in Parkinson's disease. *Eur. Neuropsychopharmacol.* 20, 784–792. doi: 10.1016/j.euroneuro.2010.07.001

Dubois, B., Slachevsky, A., Litvan, I., and Pillon, B. (2000). The FAB: a frontal assessment battery at bedside. *Neurology* 55, 1621–1626. doi: 10.1212/WNL.55.11.1621

Fahn, S., and Elton, R. (1987). "Unified Parkinson's disease rating scale," in *Recent Developments in Parkinson's Disease*, *Vol 2*, S. Fahn, C. D. Marsden, D. B. Calne, and M. Goldstein (Florham Park, NJ: Macmillan Health Care Information), 153–163, 293–304

Faul, F., Erdfelder, E., Lang, A. G., and Buchner, A. (2007). G* Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Methods* 39, 175–191. doi: 10.3758/BF03193146

Fearon, C., Butler, J., Newman, L., Lynch, T., and Reilly, R. (2015). Audiovisual processing is abnormal in Parkinson's disease and correlates with freezing of gait and disease duration. *J. Parkinsons Dis.* 5, 925–936. doi: 10.3233/JPD-150655

Gelb, D. J., Oliver, E., and Gilman, S. (1999). Diagnostic criteria for Parkinson disease. *Arch. Neurol.* 56, 33–39. doi: 10.1001/archneur.56.1.33

Gil, S., and Gilbar, O. (2001). Hopelessness among cancer patients. *J. Psychosoc. Oncol.* 19, 21–33. doi: 10.1300/J077v19n01_02

Goh, W. Y., Chan, D., Ali, N. B., Chew, A. P., Chuo, A., Chan, M., et al. (2019). Frontal assessment battery in early cognitive impairment: psychometric property and factor structure. *J. Nutr. Health Aging* 23, 966–972. doi: 10.1007/s12603-019-1248-0

Gong, B., Li, Q., Zhao, Y., and Wu, C. (2021). Auditory emotion recognition deficits in schizophrenia: a systematic review and meta-analysis. *Asian J. Psychiatr.* 65:102820. doi: 10.1016/j.ajp.2021.102820

Gothwal, M., Arumugham, S. S., Yadav, R., Pal, P. K., and Hegde, S. (2022). Deficits in emotion perception and cognition in patients with Parkinson's disease: a systematic review. *Ann. Indian Acad. Neurol.* 25, 367–375. doi: 10.4103/aian.aian_573_21

Gray, H. M., and Tickle-Degnen, L. (2010). A meta-analysis of performance on emotion recognition tasks in Parkinson's disease. *Neuropsychology* 24, 176–191. doi: 10.1037/a0018104

Green, M. F., Horan, W. P., and Lee, J. (2015). Social cognition in schizophrenia. *Nat. Rev. Neurosci.* 16, 620–631. doi: 10.1038/nrn4005

Gunnery, S. D., Habermann, B., Saint-Hilaire, M., Thomas, C. A., and Tickle-Degnen, L. (2016). The relationship between the experience of hypomimia and social wellbeing in people with Parkinson's disease and their care partners. *J. Parkinsons Dis.* 6, 625–630. doi: 10.3233/JPD-160782

Hayes, G., McLennan, S., Henry, J., Phillips, L., Terrett, G., Rendell, P.., et al. (2020). Task characteristics influence facial emotion perception age-effects: a meta-analytic review. *Psychol. Aging* 35:295. doi: 10.1037/pag0000441

Hindle, J., Martyr, A., and Clare, L. (2014). Cognitive reserve in Parkinson's disease: a systematic review and meta-analysis. *Parkinson. Relat. Disord.* 20, 1–7. doi: 10.1016/j.parkreldis.2013.08.010

Hu, Y., Baragchizadeh, A., and O'Toole, A. J. (2020). Integrating faces and bodies: psychological and neural perspectives on whole person perception. *Neurosci. Biobehav. Rev.* 112, 472–486. doi: 10.1016/j.neubiorev.2020.02.021

Israelashvili, J., Hassin, R. R., and Aviezer, H. (2019). When emotions run high: a critical role for context in the unfolding of dynamic, real-life facial affect. *Emotion* 19, 558–562. doi: 10.1037/emo0000441

Jacobs, D. H., Shuren, J., Bowers, D., and Heilman, K. M. (1995). Emotional facial imagery, perception, and expression in Parkinson's disease. *Neurology* 45, 1696–1702. doi: 10.1212/WNL.45.9.1696

Kohler, C., Walker, J., Martin, E., Healey, K., and Moberg, P. (2010). Facial emotion perception in schizophrenia: a meta-analytic review. *Schizophr. Bull.* 36, 1009–1019. doi: 10.1093/schbul/sbn192

Kring, A. M., and Elis, O. (2013). Emotion deficits in people with schizophrenia. *Annu. Rev. Clin. Psychol.* 9, 409–433. doi: 10.1146/annurev-clinpsy-050212-185538

Lecker, M., Shoval, R., Aviezer, H., and Eitam, B. (2017). Temporal integration of bodies and faces: United we stand, divided we fall? *Vis. Cogn.* 25, 477–491. doi: 10.1080/13506285.2017.1310164

Lifshitz, M., Dwolatzky, T., and Press, Y. (2012). Validation of the Hebrew version of the MoCA test as a screening instrument for the early detection of mild cognitive impairment in elderly individuals. *J. Geriatr. Psychiatry Neurol.* 25, 155–161. doi: 10.1177/0891988712457047

Lin, C., Tien, Y., Huang, J., Tsai, C., and Hsu, L. (2016). Degraded impairment of emotion recognition in Parkinson's disease extends from negative to positive emotions. *Behav. Neurol.* 2016:9287092. doi: 10.1155/2016/9287092

Lin, Y., Ding, H., and Zhang, Y. (2020). Multisensory integration of emotion in schizophrenic patients. *Multisens. Res.* 33, 865–901. doi: 10.1163/22134808-bja10016

Meder, D., Herz, D., Rowe, J., Lehéricy, S., and Siebner, H. (2019). The role of dopamine in the brain-lessons learned from Parkinson's disease. *Neuroimage* 190, 79–93. doi: 10.1016/j.neuroimage.2018.11.021

Meeren, H. K., van Heijnsbergen, C. C., and de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proc. Natl. Acad. Sci. U. S. A.* 102, 16518–16523. doi: 10.1073/pnas.0507650102

Mioshi, E., Dawson, K., Mitchell, J., Arnold, R., and Hodges, J. (2006). The Addenbrooke's Cognitive Examination Revised (ACE-R): a brief cognitive test battery for dementia screening. *Int. J. Geriatr. Psychiatry* 21, 1078–1085. doi: 10.1002/gps.1610

Newman, J. (2005). Brief assessment of cognitive mental status in Hebrew: Addenbrooke's Cognitive Examination. *IMAJ-Ramat Gan* 7:451.

Niedenthal, P. M. (2007). Embodying emotion. *Science* 316, 1002–1005. doi: 10.1126/science.1136930

Noh, S. R., and Isaacowitz, D. M. (2013). Emotional faces in context: age differences in recognition accuracy and scanning patterns. *Emotion* 13, 238–249. doi: 10.1037/a0030234

Pell, M., and Leonard, C. (2003). Processing emotional tone from speech in Parkinson's disease: a role for the basal ganglia. *Cogn. Affect. Behav. Neurosci.* 3, 275–288. doi: 10.3758/CABN.3.4.275

Péron, J., Grandjean, D., Drapier, S., and Vérin, M. (2014). Effect of dopamine therapy on nonverbal affect burst recognition in Parkinson's disease. *PLoS ONE* 9:e90092. doi: 10.1371/journal.pone.0090092

Phillips, M. L., Drevets, W. C., Rauch, S. L., and Lane, R. (2003). Neurobiology of emotion perception I: the neural basis of normal emotion perception. *Biol. Psychiatry* 54, 504–514. doi: 10.1016/S0006-3223(03)00168-9

Pierce, J. E., and Péron, J. (2020). The basal ganglia and the cerebellum in human emotion. *Soc. Cogn. Affect. Neurosci.* 15, 599–613. doi: 10.1093/scan/nsaa076

Ricciardi, L., Bologna, M., Morgante, F., Ricciardi, D., Morabito, B., Volpe, D., et al. (2015). Reduced facial expressiveness in Parkinson's disease: a pure motor disorder? *J. Neurol. Sci.* 358, 125–130. doi: 10.1016/j.jns.2015.08.1516

Ricciardi, L., Visco-Comandini, F., Erro, R., Morgante, F., Bologna, M., Fasano, A., et al. (2017). Facial emotion recognition and expression in Parkinson's disease: an emotional mirror mechanism? *PLoS ONE* 12:e0169110. doi: 10.1371/journal.pone.0169110

Sala, G., Inagaki, H., Ishioka, Y., Masui, Y., Nakagawa, T., Ishizaki, T., et al. (2020). The psychometric properties of the Montreal Cognitive Assessment (MoCA): a comprehensive investigation. *Swiss J. Psychol.* 79, 155–161. doi: 10.1024/1421-0185/a000242

Schlegel, K., Vicaria, M., and Isaacowitz, D. (2020). Facets of interpersonal accuracy across the lifespan: is there a single skill in older age? *J. Nonverb. Behav.* 1–26. doi: 10.1007/s10919-019-00326-x

Schneider, F., Althaus, A., Backes, V., and Dodel, R. (2008). Psychiatric symptoms in Parkinson's disease. *Eur. Arch. Psychiatry Clin. Neurosci.* 258(Suppl. 5), 55–59. doi: 10.1007/s00406-008-5012-4

Schröder, C., Nikolova, Z., and Dengler, R. (2010). Changes of emotional prosody in Parkinson's disease. *J. Neurol. Sci.* 289, 32–35. doi: 10.1016/j.jns.2009.08.038

Silberstein, P., Bittar, G., Boyle, R., Cook, R., Coyne, T., O'Sullivan, D., et al. (2009). Deep brain stimulation for Parkinson's disease: Australian referral guidelines. *J. Clin. Neurosci.* 16, 1001–1008. doi: 10.1016/j.jocn.2008.11.026

Simons, G., Pasqualini, M. C., Reddy, V., and Wood, J. (2004). Emotional and nonemotional facial expressions in people with Parkinson's disease. *J. Int. Neuropsychol. Soc.* 10, 521–535. doi: 10.1017/S135561770410413X

Słowiński, P., Alderisio, F., Zhai, C., Shen, Y., Tino, P., Bortolon, C., et al. (2017). Unravelling socio-motor biomarkers in schizophrenia. *npj Schizophr.* 3:8. doi: 10.1038/s41537-016-0009-x

Sonnenschein, S., Gomes, F., and Grace, A. (2020). Dysregulation of midbrain dopamine system and the pathophysiology of schizophrenia. *Front. Psychiatry* 11:613. doi: 10.3389/fpsyt.2020.00613

Takenoshita, S., Terada, S., Yoshida, H., Yamaguchi, M., Yabe, M., Imai, N., et al. (2019). Validation of Addenbrooke's cognitive examination III for detecting mild cognitive impairment and dementia in Japan. *BMC Geriatr.* 19, 1–8. doi: 10.1186/s12877-019-1120-4

Thoma, P., Soria Bauser, D., and Suchan, B. (2013). BESST (Bochum Emotional Stimulus Set)—a pilot validation study of a stimulus set containing emotional bodies and faces from frontal and averted views. *Psychiatry Res.* 209, 98–109. doi: 10.1016/j.psychres.2012.11.012

Trémeau, F. (2022). A review of emotion deficits in schizophrenia. *Dialog. Clin. Neurosci.* 8, 59–70. doi: 10.31887/DCNS.2006.8.1/ftremeau

van der Schalk, J., Hawk, S., Fischer, A., and Doosje, B. (2011). Moving faces, looking places: validation of the Amsterdam Dynamic Facial Expression Set (ADFES). *Emotion* 11, 907–920. doi: 10.1037/a0023853

Vannuscorps, G., Andres, M., and Caramazza, A. (2020). Efficient recognition of facial expressions does not require motor simulation. *Elife* 9:e54687. doi: 10.7554/eLife.54687.sa2

Walther, S., van Harten, P. N., Waddington, J. L., Cuesta, M. J., Peralta, V., Dupin, L., et al. (2020). Movement disorder and sensorimotor abnormalities in schizophrenia and other psychoses - European consensus on assessment and perspectives. *Eur. Neuropsychopharmacol.* 38, 25–39. doi: 10.1016/j.euroneuro.2020.07.003

Wang, P., and Gorenstein, C. (2013). Psychometric properties of the Beck Depression Inventory-II: a comprehensive review. *Braz. J. Psychiatry* 35, 416–431. doi: 10.1590/1516-4446-2012-1048

Wieser, M., and Brosch, T. (2012). Faces in context: a review and systematization of contextual influences on affective face processing. *Front. Psychol.* 3:471. doi: 10.3389/fpsyg.2012.00471

Winkielman, P., Niedenthal, M., and Oberman, L. (2008). "The embodied emotional mind," in *Embodied Grounding: Social, Cognitive, Affective, and Neuroscientific Approaches*, eds G. R. Semin, and E. R. Smith (Cambridge: Cambridge University Press), 263–288.

Wood, A., Rychlowska, M., Korb, S., and Niedenthal, P. (2016). Fashioning the face: sensorimotor simulation contributes to facial expression recognition. *Trends Cogn. Sci.* 20, 227–240. doi: 10.1016/j.tics.2015.12.010

frontiers | Frontiers in Psychology

TYPE Original Research
PUBLISHED 23 May 2024
DOI 10.3389/fpsyg.2024.1281857

OPEN ACCESS

EDITED BY
Florin Dolcos,
University of Illinois at Urbana-Champaign,
United States

REVIEWED BY
Kentaro Katahira,
National Institute of Advanced Industrial
Science and Technology (AIST), Japan
Takashi Tsukiura,
Kyoto University, Japan
Hirokazu Doi,
Nagaoka University of Technology, Japan

*CORRESPONDENCE
Shushi Namba
✉ nashushi@hiroshima-u.ac.jp

RECEIVED 24 August 2023
ACCEPTED 07 May 2024
PUBLISHED 23 May 2024

CITATION
Namba S, Saito A and Sato W (2024) Computational analysis of value learning and value-driven detection of neutral faces by young and older adults.
Front. Psychol. 15:1281857.
doi: 10.3389/fpsyg.2024.1281857

Computational analysis of value learning and value-driven detection of neutral faces by young and older adults

Shushi Namba[1,2]*, Akie Saito[1] and Wataru Sato[1]

[1]Psychological Process Team, Guardian Robot Project, RIKEN, Kyoto, Japan, [2]Department of Psychology, Hiroshima University, Hiroshima, Japan

The rapid detection of neutral faces with emotional value plays an important role in social relationships for both young and older adults. Recent psychological studies have indicated that young adults show efficient value learning for neutral faces and the detection of "value-associated faces," while older adults show slightly different patterns of value learning and value-based detection of neutral faces. However, the mechanisms underlying these processes remain unknown. To investigate this, we applied hierarchical reinforcement learning and diffusion models to a value learning task and value-driven detection task that involved neutral faces; the tasks were completed by young and older adults. The results for the learning task suggested that the sensitivity of learning feedback might decrease with age. In the detection task, the younger adults accumulated information more efficiently than the older adults, and the perceptual time leading to motion onset was shorter in the younger adults. In younger adults only, the reward sensitivity during associative learning might enhance the accumulation of information during a visual search for neutral faces in a rewarded task. These results provide insight into the processing linked to efficient detection of faces associated with emotional values, and the age-related changes therein.

KEYWORDS

facial expression detection, associative learning, diffusion model, emotional value, gerontology

1 Introduction

The ability to efficiently determine the emotional significance of facial expressions is crucial for adaptive behavior in social interactions (Stins et al., 2011; Heerdink et al., 2015). Efficient detection of faces with positive emotional value is important for social behaviors and relationships. Similarly, rapid detection of faces displaying negative, threatening emotions can enable an individual to avoid a dangerous situation and preserve resources.

The adaptive qualities of emotional expressions appear to influence attention (Hansen and Hansen, 1988; Fenske and Raymond, 2006; Craig et al., 2014). However, this idea has led to several controversies in the field of psychology (Puls and Rothermund, 2018; Tannert and Rothermund, 2020). For example, there is conjecture regarding the physical and emotional significance of faces providing emotional information (Horstmann et al., 2006; Calvo and Nummenmaa, 2008; Horstmann et al., 2012). To control for perceptual properties when investigating the detection of faces with emotional information, Saito et al. (2022a) employed inherently neutral faces associated with positive or negative values as target stimuli in a visual search task. They based their paradigm on an associative learning task in which neutral stimuli (e.g., colors) were linked with a reward or punishment (Anderson et al., 2011; Wentura et al., 2014; Muller et al., 2016). They found that the reaction time (RT) during a visual search for neutral faces associated with a reward or punishment was reduced compared with that for neutral faces not associated with feedback. In other words, emotional significance facilitated attentional capture during a visual search task.

Given the aging of many contemporary societies, the cognition of older adults has been a major research focus (Ziaei and Fischer, 2016). Older people exhibit a "positivity effect," i.e., they tend to focus their attention on pleasant stimuli (Reed et al., 2014). However, studies on this topic have yielded inconsistent results. For example, a recent study (Saito et al., 2020) found that both young and older participants readily attended to angry facial expressions. In contrast, older participants did not show this tendency for happy facial expressions. In addition, in an associative learning task combined with a visual search paradigm, Saito et al. (2022b) found that positive (reward) and negative (punishment) outcomes in the associative learning task facilitated attention in the visual search task for successful young and older learners, although there were no differences in emotional valence.

Although previous studies have demonstrated rapid detection of neutral faces associated with an emotional value (Saito et al., 2022a,b), the mechanism underlying the relationship between associative learning and visual search attention remains unclear. Visual search performance has been investigated in successful and unsuccessful learners. However, several scholars have pointed out that such binary groupings are statistically undesirable (DeCoster et al., 2009; Reinhart, 2015). The RT, as a dependent variable, is inherently right-skewed. Analysis of variance (ANOVA), which assumes a normal data distribution, is also inappropriate for this type of study. Another problem is that classification errors are generally analyzed separately from RT, making it impossible to assess the speed-accuracy trade-off. Furthermore, the RTs regarding the relationship between associative learning rate and visual search performance were not compared between the groups because the groups were distinguished using a binary classification scheme based on the associative learning performance (Saito et al., 2022a,b).

Computational modeling using behavioral data has potential for elucidating the mechanisms of human psychological processes (Lee and Wagenmakers, 2014). The reinforcement learning model (Rescorla and Wagner, 1972; Hertwig et al., 2004) can be used to quantitatively evaluate learning rate parameters in learning tasks, and to reveal their associations with other variables and obtain insight into the mechanisms of human behaviors (e.g., Dombrovski et al., 2010; Kwak et al., 2014; Suzuki et al., 2023). Given the above findings, reinforcement learning is likely to be useful for examining performance in learning tasks that involve associative learning; they allow the identification of factors that contribute to success in learning tasks, such as sensitivity to feedback (η) or reliance on a model (τ).

The diffusion model (Ratcliff, 1978; Ratcliff and Rouder, 1998; Ratcliff and McKoon, 2008; Forstmann et al., 2016) can be used to describe the distribution of RTs associated with the detection of emotional faces (Tipples, 2019; Sawada et al., 2022). The diffusion model includes four main parameters. The threshold separation (α) is the distance between two choices (i.e., target presence and absence), z denotes the starting point (which is related to prior bias in two-choice tasks), and ν is the drift rate (speed with which evidence is accumulated in relation to a specific response, i.e., toward the upper or lower threshold). The non-decision time (t0) is based on all time components unrelated to the information accumulation process. RTs tend to be classified as fast or slow in experimental tasks. However, more in-depth metrics can be obtained, such as the speed with which information is accumulated (ν), the amount of information required (α), and the time required to arrive at a judgement (t0). Analysis of such metrics can reveal the mechanisms underlying psychological processes. Indeed, Sawada et al. (2022) used the diffusion model to estimate cognitive parameters in a visual search task requiring participants to detect angry and happy expressions, and their anti-expressions, within a crowd of neutral faces. Regardless of valence, ν for emotional facial expressions was rapid, α values were large, and t0 values were small. These results suggest that efficient detection of facial expressions is characterized by the faster and more cautious accumulation of information through enhanced attentional allocation.

When investigating the relationships among different behavioral task performance indices, a computational modeling approach can be used to maximize the amount of information obtained. By fitting a reinforcement learning model to associative learning data and a diffusion model to visual search data, and then examining the relationship between the resulting parameters, further insight can be obtained into the mechanisms underlying the detection of faces with emotional meaning.

In this study, we explored the psychological processes underlying the rapid detection of faces with emotional meaning by investigating the relationship between associative learning and visual search data. Moreover, we investigated developmental changes by comparing young and older participants. We applied the hierarchical reinforcement learning and diffusion models to data collected in previous studies (Saito et al., 2022a,b) (Figure 1). Then, we checked the relationships between the resulting parameters using both models. Learning success in associative learning tasks was quantitatively represented by changes in learning rates on a continuum, instead of a binary classification. We also calculated three psychologically meaningful parameters (α, ν, and t0) instead of the RT. This study is the first to investigate the relationships among the above parameters.

We tested three hypotheses using computational models. The first hypothesis was informed by the previous finding that people tend to avoid negative situations rather than to show approach behavior to positive ones. Kahneman and Tversky (1979) explained this asymmetry between gain and loss using prospect theory. Katahira et al. (2011) revealed that the negative reward value of negative pictures was larger than the positive reward value of positive pictures. Thus, we expected the learning rate in the associative learning task to be higher in both younger and older participants for punishment trials than reward trials. In terms of developmental changes, Saito et al. (2020) reported that older participants showed markedly reduced sensitivity to positive expressions compared with younger participants. Thus, our hypotheses are as follows: 1–1. Learning rate parameters will be higher for punishment trials than reward trials. 1–2. Older participants will have low learning rates for rewards. In the visual search paradigm, we expected the younger group to exhibit superior performance compared with the older group (Salthouse, 2000). Accordingly, we hypothesized that each diffusion model parameter value will be higher in the younger participants than in the older ones. Finally, based on a straightforward interpretation of Saito et al. (2022b), we predicted that the ν in RT will be linked to the learning rates. The relationships between other parameters were investigated in an exploratory manner.

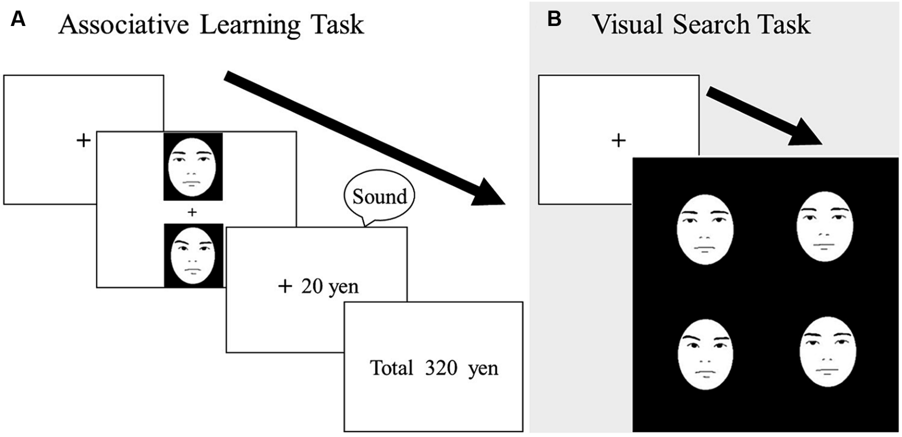


FIGURE 1
Schematic illustrations of trials in the learning task **(A)** and visual search task **(B)**. In the learning task, participants chose one face from each pair to maximize their earnings. In the visual search task, participants identified one discrepant face embedded among distractor faces. Actual stimuli were photographic faces.

2 Methods

2.1 Participants

We recruited 29 young adult participants (13 women; mean ± SD age = 22.6 ± 2.1 years), all of whom were either undergraduate or graduate students at Kyoto University. We also recruited 32 older participants (16 women; mean ± SD age = 73.5 ± 5.3 years) from a local human resource center in Kyoto. All participants were paid for their participation. The sample size was determined by *a priori* power analysis, using a frequentist approach with an assumed α level because the data had been used in previous studies (Saito et al., 2022a,b). All participants provided written informed consent to take part in the study, which was approved by the ethics committee of the Unit for Advanced Studies of the Human Mind at Kyoto University and conducted in accordance with institutional ethical guidelines and the Declaration of Helsinki.

2.2 Stimuli

Seven grayscale images of male faces with neutral expressions were selected from a database containing 65 faces of Japanese individuals (Sato et al., 2019). One face was used as a distractor in the visual search task, and the others were used as targets in the associative learning and visual search tasks. The images were adjusted for brightness and contrast using Photoshop 5.0 (Adobe, San Jose, CA) and the mean luminance was equalized using MATLAB R2017b (MathWorks, Natick, MA). The stimuli were controlled in terms of both attractiveness and distinctiveness. The detection speed was not significantly different between the target faces in the visual search task according to the results of preliminary experiments ($F(5,35) = 2.18$, $p = 0.079$). All stimuli were cut into ellipses to exclude distinctive factors (e.g., hairstyle and facial contours), and had subtended visual angles of 3.5° horizontally × 4.5° vertically.

2.2.1 Associative learning task

Three pairs of faces were used. The face pairs were fixed throughout the learning task. Each pair was allocated to one of the three value conditions (reward, punishment, or zero outcome), and this allocation was counterbalanced across participants. In the reward and punishment conditions, one face in each pair was designated as the target. Selecting the target resulted in a monetary reward (20 yen increase in each trial) or punishment (20 yen decrease in each trial) in 80% of trials (zero outcomes for the other 20%). The nontarget image in each pair was assigned the reverse probability pattern (i.e., 20% probability of monetary reward or punishment). In the zero-outcome condition, one face was the target, but the monetary outcome was always zero regardless of whether the participants selected the target or nontarget. This condition was set as a control condition to compare the learning conditions (reward and punishment). The target face statuses in each condition were counterbalanced across the participants. Each participant experienced 1 of 24 stimulus presentation combinations in the learning task.

2.2.2 Visual search task

The same three face pairs from the associative learning task were used in the visual search task. The face classified as the target in each condition in the associative learning task was also the target in this task. An additional face with a neutral expression was used as a distractor. The search display was a square (11.0° × 11.0°) within which faces were presented in four positions at 4° intervals. One target face and three identical distractor faces were presented in each of the four positions in the target-present condition. Each target face was presented 8 times in each of the four positions, so that each target was presented 32 times in total. In the target-absent condition, the four identical distractor faces appeared in all of the positions.

2.3 Procedure

The participants were seated in a chair with a chin rest fixed 80 cm from the monitor. The experimental room was soundproofed and dimly lit.

2.3.1 Associative learning task

The participants took part in a betting game, in which they were asked to choose a face from each stimulus pair based on their "gut feeling" and register their response by pressing the corresponding button on a response box. The goal of the task was to maximize their earnings. Because the participants were not told which of the paired faces was the target, they had to make a guess about which face would be more likely to lead to a reward. They were informed that the money they earned would be paid after the experiment, and were asked to try and earn as much money as possible. Each trial began with the presentation of a fixation cross for 500 m, followed by a pair of faces. The faces in the pair were positioned 2.5° above or below the fixation cross (0.9° × 0.9°), such that they appeared in the center of the screen. The positions of the target and nontarget faces were pseudo-randomized. After the participant made a response, a "reward" message (plus 20 yen, minus 20 yen, or 0 yen) was presented on the screen, and a sound indicated whether the answer was correct or incorrect (no sound for 0 yen). Then, the amount of money earned was displayed on the screen for 1,800 ms. Each face pair was presented 10 times (total of 30 trials) in one block, and there were 10 blocks in the main experiment, resulting in 300 trials. To prevent the consecutive presentation of identical face pairs in the same position, the presentation order of the face pairs was pseudo-randomized. Prior to the experiment, the participants completed 30 practice trials to familiarize themselves with the task.

2.3.2 Visual search task

Before the experiment, the participants were informed that no monetary reward or punishment would occur in this task. In each trial, a fixation cross was shown for 500 ms, followed by a stimulus array containing four faces (Figure 1B) that did not have any facial movements (i.e., neutral faces). The participants were instructed to indicate whether one of the faces was dissimilar from the others, or if all four faces were the same, by pressing the corresponding button on the response box as quickly and accurately as possible. The allocation of the response buttons was counterbalanced across participants. Each block included 24 target-present trials (8 trials each in the reward, punishment, and zero-outcome conditions) and 24 target-absent trials. The main experiment consisted of four blocks, such that the total number of trials was 192. To prevent the consecutive presentation of identical targets in the same position, the order of trial presentation was pseudo-randomized in each block. There was no time limit. Before the experiment, the participants completed 24 practice trials.

In the associative learning task, two younger participants (−220 ~ −140 yen) and 10 older participants (−440 ~ −20 yen) had net negative amounts. Regardless of whether a negative or positive amount of money was earned, all participants received the same predetermined monetary bonus in the learning task (1,000 Japanese yen) after they had been debriefed.

2.4 Statistical approach

2.4.1 Associative learning task

To determine whether the learning conditions affected face selection, and whether that effect differed depending on age, we performed three-way mixed ANOVA with factors of learning condition (reward, punishment and zero), trial block (1–20, 21–40, 41–60, 61–80, and 81–100), and age (younger and older). For *post-hoc* tests, *p*-values were adjusted using the Holm-Bonferroni sequentially rejective procedure (Holm, 1979). Learning was assumed to have occurred, if there was a performance difference between the first 20 and final 20 trials.

To build a reinforcement learning model, we established a modified multiple-armed bandit model (Hertwig et al., 2004; Ahn et al., 2017) based on the Rescorla-Wagner (delta) model in which the learning rates for reward and punishment were distinguished (Rescorla and Wagner, 1972). Because there was no feedback in the zero condition, the estimates were not uniquely determined; we used only the data for the reward and punishment conditions. Thus, we estimated four main parameters: the learning rate for reward (η_r), learning rate for punishment (η_p), inverse temperature for reward (τ_r), and inverse temperature for punishment (τ_p). First, we set four expected values for the four choices (target face choice in reward conditions, nontarget face choice in reward conditions, target face choice in punishment conditions, and nontarget face choice in punishment conditions). Next, we calculated prediction error (PE) by subtracting the monetary outcome (+1, 0, −1) from the expected value (EV) for each choice. After that, the following updating rule was formulated.

$$EV_{new} = EV_{old} + \eta_r * PE \text{ for reward}$$

$$EV_{new} = EV_{old} + \eta_p * PE \text{ for punishment}$$

To calculate the action probabilities, we used the softmax choice rule with the inverse temperature parameter (τ_r, τ_p), which reflects how individuals' choices are made deterministically with respect to the value of the alternative choices (Kaelbling et al., 1996). An increase in the inverse temperature corresponds to a preference for model dependent choices, whereas a decrease in the inverse temperature reflects a tendency toward more random decisions. The learning rates represent the sensitivity of feedback in a learning task, where η close to 1 places more weight on recent outcomes.

In addition, we applied Bayesian hierarchical modeling (Lee and Wagenmakers, 2014), which can delineate individual differences and similarities among participants and thus enhance the accuracy of statistical inferences (Gelman and Hill, 2006; Driver and Voelkle, 2018; Namba et al., 2022). The number of iterations was set to 5,000, the number of burn-in samples to 5,000, and the number of chains to four. The R-hat value for all parameters was 1.0, indicating convergence of the four chains (Stan Development Team, 2020). The details of the model, including the prior distributions, are described in the Supplementary material.[1]

2.4.2 Visual search task

To determine whether the learning conditions affected visual search performance (i.e., RT and accuracy), and whether that effect differed by age, we performed two-way mixed ANOVA including learning condition (reward, punishment and zero) and age (younger and older). Similar to the associative learning tasks, *p*-values were adjusted using the Holm-Bonferroni sequentially rejective procedure. We were concerned with the difference between the reward,

---

[1] https://osf.io/rw3e4/

punishment, and no feedback conditions in the target-present trials, rather than the difference between the target-present and absent conditions. Thus, we focused on the target-present condition in the visual search task.

To build the hierarchical drift-diffusion model, we applied a response-fitting model that use two outputs: same or dissimilar. We extracted the three main parameters from the behavioral data using the hierarchical drift diffusion model: α, v, and t0. For parameter estimation, we calculated individual-level parameters (and the within-condition covariance structure) for α, v in the different learning conditions (reward, punishment, and zero), and we calculated a population-level parameter for t0. z was fixed at 0.5. This was due to the need to constrain parameters for stable convergence (Kinosada, 2019). We determined whether the values of R-hat were close to 1 (values closer to 1 indicate greater convergence) and calculated the variation between the four chains (smaller variance reflects greater convergence). The number of iterations was set to 5,000, and the number of burn-in samples was set to 5,000. The diffusion model, including the prior distributions, was described in detail in (see Footnote 1).

Finally, we explored the correlations among the underlying parameters for each participant. Since no sample size calculation or *a priori* power analysis was conducted, we used conservative criteria, i.e., $r > 0.30$ (Cohen, 2013). All analyses were performed using R ver. 3.6.1 (R Core Team, 2019), with the "anovakun," "bayesplot," "brms," "cmdstanr," "posterior," "rstan," "tidyverse" packages (Bürkner, 2017; Gabry et al., 2019, 2023; Wickham et al., 2019; Stan Development Team, 2020; Bürkner et al., 2023; Iseki, 2023).

3 Results

3.1 Associative learning task

First, we checked the learning curves for the young and older participants, as shown in Figure 2. A visual inspection of the performance of the younger and older participants indicated good learning outcomes in both groups, although the younger participants exhibited more efficient learning. Three-way mixed ANOVA was performed to evaluate the effects of age, learning and trial block. There was no main effect of age or trial block, and interaction effect between age and trial block (Fs < 0.35, ps > 0.55, η_G^2s < 0.002), but the main effect of learning condition was significant ($F(2, 110) = 49.61$, $p < 0.001$, $\eta_G^2 = 0.32$). Participants in the reward condition performed significantly better than those in the zero and punishment conditions, and participants in the zero condition performed better than those in the punishment condition (ts > 4.36, ps < 0.001). There was also an interaction effect between trial block and learning condition ($F(8, 440) = 13.43$, $p < 0.001$, $\eta_G^2 = 0.05$). The *post hoc* test showed significant differences between trial blocks in the reward and punishment conditions (Fs > 14.22, ps < 0.001, η_G^2s > 0.06), but there was no difference between trial blocks in the zero condition ($F(4, 220) = 0.38$, $p = 0.82$, $\eta_G^2 = 0.00$). In the reward condition, the selection rate was significantly higher in the last 20 trials than in the first 20 trials ($t = 5.04$, $p < 0.001$), but the opposite was true in the punishment condition ($t = 5.30$, $p < 0.001$). This indicates that associative learning for reward and punishment occurred in both participants. In addition, there was an interaction effect between age and learning condition ($F(7, 43) = 7.43$, $p = 0.001$, $\eta_G^2 = 0.07$). The *post hoc* test showed significant differences between younger and older participants in the reward and punishment conditions (Fs > 9.25, ps < 0.004, η_G^2s > 0.10), with the effects being smaller in older than younger participants, but there was no difference in the zero condition ($F(1,55) = 0.02$, $p = 0.88$, $\eta_G^2 = 0.00$). Moreover, the performance of younger participants significantly differed among the conditions; performance was best in the reward condition, followed by the zero condition and finally by the punishment condition (ts > 5.40, ps < 0.001). Older participants performed worse in the punishment condition than the other two learning conditions (ts > 2.76, ps < 0.02), but the reward condition did not differ from the zero condition ($t = 1.35$, $p = 0.19$). In summary, the younger participants were able to learn reward and punishment contingencies in the associative learning task, and the older participants were able to learn punishment contingencies in the associative learning task but not reward contingencies.

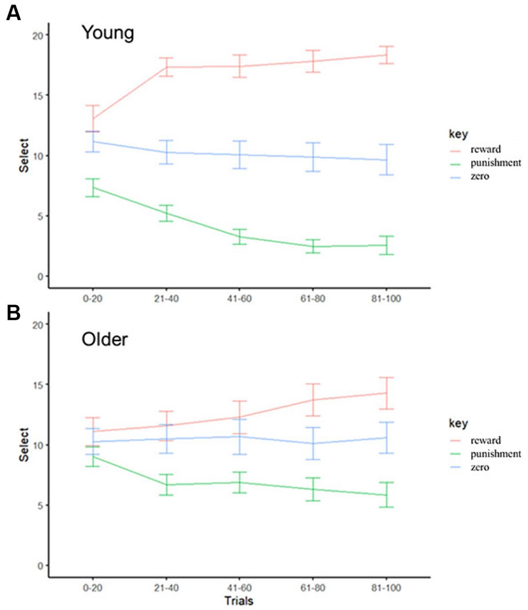


FIGURE 2
(A) Mean (± standard error) proportion of target faces selected by younger participants for each block (1–20) in the reward, punishment and zero conditions. **(B)** Mean (± standard error) proportion of target faces selected by older participants for each block (1–20 trials) in the reward, punishment, and zero conditions.

Next, as shown in Table 1 and Figure 3, we assessed the results for the reinforcement learning model parameters. There was a small difference in learning rate between the reward and punishment trials among the younger participants. Specifically, the learning rates were higher for punishment trials. For the inverse temperature parameters, both groups had higher values for the reward compared with punishment trials. We performed the posterior predictive check, comparing simulated and real data (Supplementary Figure S1[2]).

Figure 4 shows the posterior distributions of each parameter difference between younger and older participants. There were

---

[2] https://osf.io/kdxz6

differences between the younger and older participants in learning rates but not inverse temperatures. Specifically, younger participants had higher learning rates than older ones (reward: mean of group difference = 0.04, 95% credible interval [CI] = [0.02, 0.07]; punishment: mean of group difference = 0.10, 95% CI = [0.04, 0.16]). There were no differences in inverse temperatures between the younger and older participants (reward: mean of group difference = −3.71, 95% CI = [−8.80, 0.38]; punishment: mean of group difference = 0.55, 95%CI = [−0.72, 1.84]).

TABLE 1 All parameters in the reinforcement-learning model.

Name	Mean	95% Credible Intervals
Younger participants		
η_{reward}	0.05	[0.03, 0.08]
$\eta_{punishment}$	0.12	[0.07, 0.19]
τ_{reward}	7.98	[6.71, 9.65]
$\tau_{punishment}$	4.50	[3.66, 5.46]
$\eta_{rew} - \eta_{pun}$	−0.07	[−0.14, −0.01]
$\tau_{rew} - \tau_{pun}$	3.48	[1.85, 5.35]
Older participants		
η_{reward}	0.01	[0.00, 0.02]
$\eta_{punishment}$	0.02	[0.01, 0.05]
τ_{reward}	11.70	[7.98, 16.70]
$\tau_{punishment}$	3.95	[3.09, 4.89]
$\eta_{rew} - \eta_{pun}$	−0.02	[−0.04, 0.00]
$\tau_{rew} - \tau_{pun}$	7.75	[3.89, 12.80]

3.2 Visual search task

To check the performance of the visual search task, we performed two-way mixed ANOVA including age and learning condition. It should be noted that this ANOVA analysis was a preliminary analysis to measure the tendency of the data. Regarding RT, there were main effects of age and learning condition (Fs > 4.45, ps < 0.02, η_G^2s > 0.01). Younger participants (mean = 0.97) showed shorter RTs than older participants (mean = 1.58; t = 8.77, p < 0.001). Regarding the effect of learning condition, RT was significantly shorter in the reward condition than in the zero condition (t = 2.96, p = 0.01), and there was a trend toward a difference between the punishment and zero conditions (t = 1.78, p = 0.08). There was no interaction effect between age and learning condition (F(2, 110) = 2.03, p = 0.14, η_G^2 = 0.005). Regarding accuracy, no significant main or interaction effects were found (Fs < 0.80, ps > 0.45, η_G^2s < 0.006). In summary, in the visual search task, the younger participants were faster than the older ones. Moreover, the RT in the reward condition, but not in the punishment condition, was significantly different to that in the zero condition over the two age groups.

As described above, we computed the three drift diffusion parameters (α, ν, t0) from the visual search data for the younger and older participants. Figure 5 shows the α values, i.e., the threshold of accumulated evidence for all conditions (two groups: younger and older; three conditions: reward, punishment, and zero). Visual inspection indicated no differences among the reward, punishment,

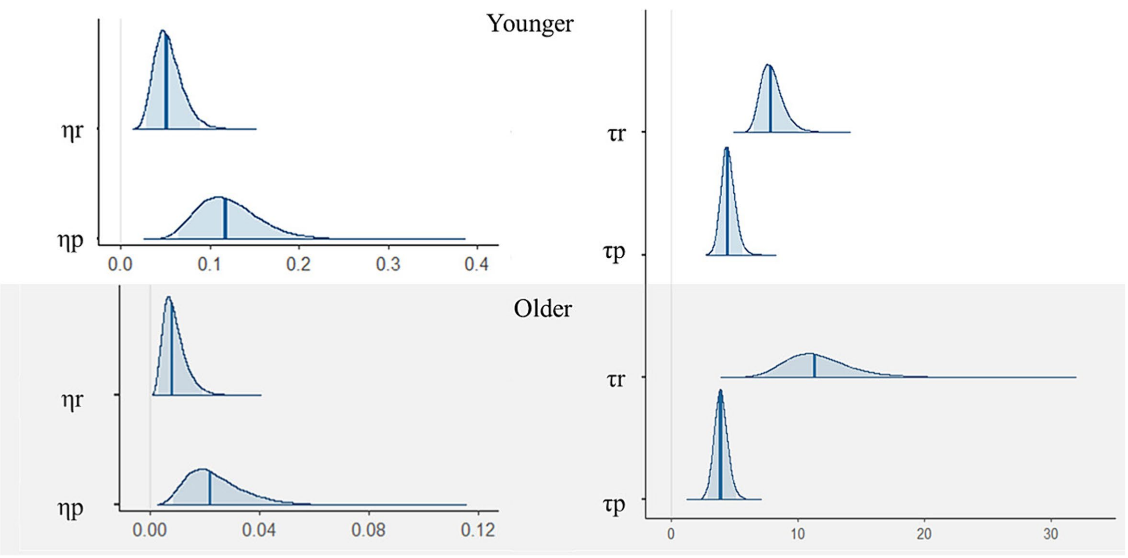


FIGURE 3
Posterior distributions of each parameter of the reinforcement learning model among younger (upper) and older participants (lower). Blue bars are expected *a posteriori* values and transparent blue regions are 95 credible intervals. η = the learning rates, τ = the inverse temperature, $*r$ = for reward, $*p$ = for punishment.

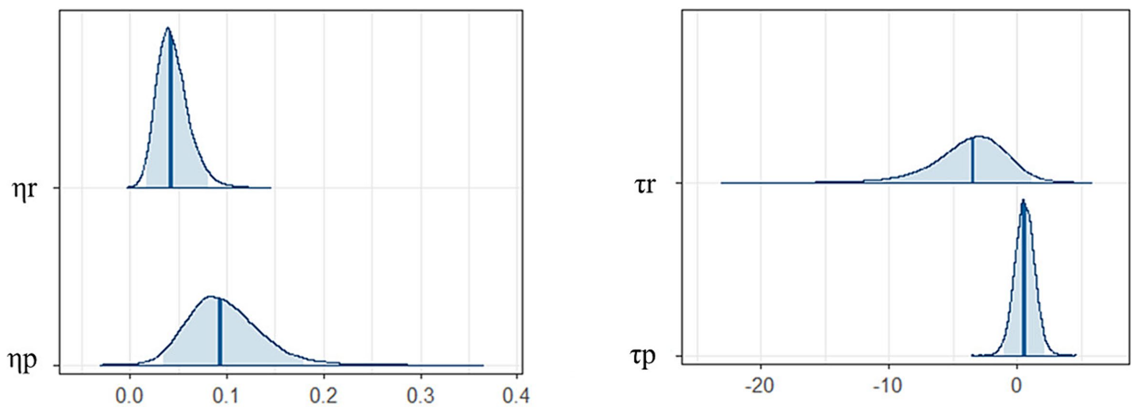


FIGURE 4
Posterior distributions of each parameter difference between younger and older participants. Blue bars are expected *a posteriori* values and transparent blue regions are 95% credible intervals. Positive values are a relatively large component of younger participants, while negative values are a relatively large component of older participants. η = the learning rates, τ = the inverse temperature, **r* = for reward, **p* = for punishment.

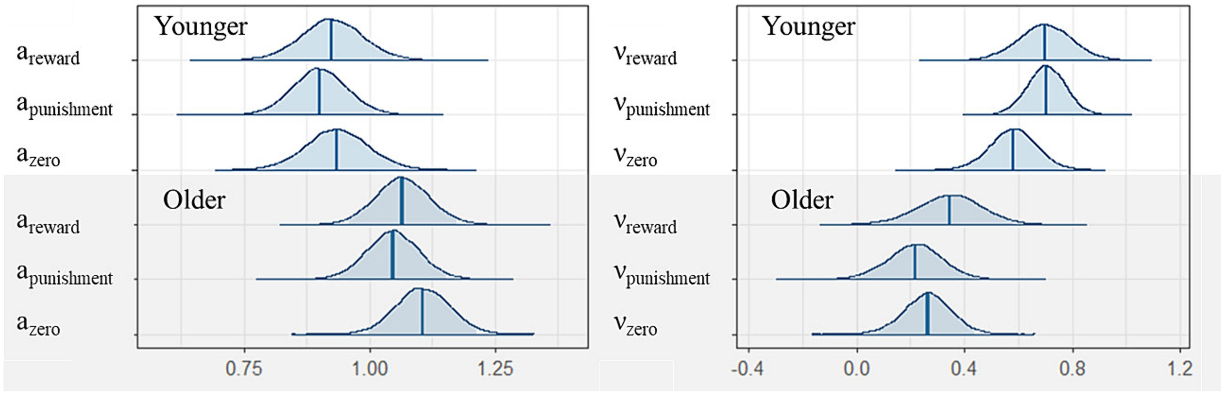


FIGURE 5
Posterior density plot of the group means of the six parameters as produced in the group (y = younger, o = older) and conditions (reward, punishment, and zero). Left: the threshold separation (α), right: the drift rate (ν).

and zero conditions, but there were differences between the younger and older participants only for the zero condition (a_{reward}: mean of group difference = −0.14, 95% credible interval [CI] = [−0.31, 0.02]; a_{loss}: mean of group difference = −0.15, 95% credible interval [CI] = [−0.30, 0.01]; a_{zero}: mean of group difference = −0.17, 95% credible interval [CI] = [−0.34, −0.01]). These results indicate that the older participants needed more information before they made a response regarding the value-driven unlearned faces. The posterior predictive check was further confirmed using reaction time values in the simulated and real data of younger and older participants [Supplementary Figure S2; (see Footnote 2)].

Figure 5 shows the results for ν, i.e., the speed at which the participants accumulated evidence before making a response. Even in the younger group, although visual inspection indicated that the positive and negative learning conditions had a relatively higher ν compared with the zero condition, performance did not differentiate positive and negative learning conditions from the zero condition ($\nu_{rew\_to\_zero}$: mean of group difference = 0.12, 95% credible interval [CI] = [−0.05, 0.28]; $\nu_{loss\_to\_zero}$: mean of group difference = 0.12, 95% credible interval [CI] = [−0.07, 0.31]). There were differences between the younger and older participants (ν_{reward}: mean of group difference = 0.35, 95% credible interval [CI] = [0.05, 0.66]; ν_{loss}: mean of group difference = 0.49, 95% credible interval [CI] = [0.24, 0.74]; ν_{zero}: mean of group difference = 0.32, 95% credible interval [CI] = [0.08, 0.57]).

t0 is based on all time components unrelated to the information accumulation process, as stated previously. There were differences between the younger and older participants ($t0_{younger}$: mean = 0.36, 95% credible interval [CI] = [0.35, 0.36]; $t0_{older}$: mean = 0.50, 95% credible interval [CI] = [0.49, 0.52]; $t0_{diff}$: mean of group difference = −0.15, 95% credible interval [CI] = [−0.16, −0.13]). In other words, older participants needed more time both before and after information accumulation than younger adults.

3.3 Relationships between associative learning and visual search parameters

To avoid the influence of outliers, we explored the Spearman's rank correlation coefficients among the underlying parameters for each participant. We extracted the mode value (most probable value) for each individual parameter. Tables 2, 3 show the relationships between associative learning and visual search parameters. In younger participants, only the learning rate in rewarded associative learning trials was correlated with the ν for faces in the reward condition ($r = 0.38$, $p = 0.04$). However, there were no other correlations between the associative learning and visual search task parameters ($|r|$s < 0.35, ps < 0.07). For older participants, there were no correlations between the associative learning and visual search task parameters ($|r|$s < 0.32, ps < 0.10).

TABLE 2 Spearman's rank correlation coefficients between the underlying mode parameters from the reinforcement-learning and drift diffusion models for younger participants.

Variable		η_r	η_p	τ_r	τ_p
a(r)	Spearman's *r*	0.23	−0.05	0.20	−0.18
a(p)	Spearman's *r*	0.13	−0.04	0.21	−0.14
a(zero)	Spearman's *r*	0.16	−0.04	0.13	−0.19
v(r)	Spearman's *r*	**0.38**	**0.32**	0.28	−0.07
v(p)	Spearman's *r*	0.11	**0.34**	0.26	0.27
v(zero)	Spearman's *r*	0.23	**0.35**	0.24	−0.05

The bold values mean significant effects or significant trends.

TABLE 3 Spearman's rank correlation coefficients between the underlying mode parameters from the reinforcement-learning and drift diffusion models for older participants.

Variable		η_r	η_p	τ_r	τ_p
a(r)	Spearman's *r*	−0.14	−0.14	−0.04	−0.29
a(p)	Spearman's *r*	0.03	−0.06	0.09	−0.17
a(zero)	Spearman's *r*	−0.01	−0.24	0.03	−0.11
v(r)	Spearman's *r*	−0.11	0.19	−0.15	−0.14
v(p)	Spearman's *r*	−0.01	0.28	−0.19	−0.12
v(zero)	Spearman's *r*	−0.06	0.32	−0.28	−0.14

4 Discussion

This study explored the psychological processes underlying the rapid detection of faces with emotional meaning by investigating the relationship between associative learning data and visual search data. First, we found that the learning rates for reward and punishment were higher for younger than older participants (Figure 4). This was consistent with the simple learning performances revealed by Figure 2. The results also showed that learning rate parameter values were higher for punishment than reward trials in younger participants only. Older participants did not show different learning rates between reward and punishment trials. This result is consistent with previous studies showing that aging reduces sensitivity to negative faces and information (Mill et al., 2009; Zhao et al., 2016; Richoz et al., 2018). Our results suggest that the sensitivity of learning feedback might decrease with age.

Both the younger and older participants in this study showed higher inverse temperatures for reward than for punishment, and there was no difference between younger and older participants for this parameter (Figure 4). The inverse temperature parameter reflects the degree to which an individual retains their previous learning history (Katahira, 2015). Thus, both younger and older participants could have kept learning history and learning rate updates in the reward trials than punishment trials. However, the younger participants may have adjusted for this difference in sensitivity (i.e., higher learning rate for punishment than reward). Our reinforcement learning model shed light on the associative learning process in both younger and older participants.

For the visual search paradigm, ν was larger and t0 was smaller in the younger group than in the older group, consistent with our hypothesis. This result is consistent with Saito et al. (2022a), who revealed that RT in visual search tasks differs between younger and older adults. This finding further demonstrates that the younger group had superior efficiency in terms of information accumulation (ν) compared to the older group. Additionally, the perceptual time leading to motion onset (t0) was shorter in the younger group. Aging might reduce the speed with which information accumulates and attention is allocated to value-associated faces. Only in the zero condition, the older participants needed more information before they made a response (α) compared to the younger participants. This could be interpreted as that the older participant's learning in the associative learning task affected the amount of information needed before they made a response, even if only slightly, so that they no longer differed from the younger participants. Figure 5 also shows that the threshold parameters for the value-driven conditions in the older participants were closer to the left than in the zero condition. The decline in performance among older participants is amenable to decomposition across distinct components as the current study indicated. The identification and elucidation of requisite interventions tailored to these specific components entail the pursuit of future research investigations.

We hypothesized that the ν for RT would be linked to each learning rate parameter. However, our results only partially supported this prediction, with the data from the younger participants in the reward condition. The result implies that sensitivity to reward in an associative learning task facilitates the accumulation of information in a visual search task for younger, but not older, participants. During an experiment in which a learning task and visual search were performed in relatively rapid succession, short term reward sensitivity was advantageous, although this effect diminished with age. This finding suggests that, in the context of building social relationships, more efficient accumulation of reward information is required in earlier stages of development. It is important to note that no such relationship was found between t0 and α. In the older participants, there were no correlations between the parameters from the two computational models. Thus, further research using a visual search task with more appropriate connections to associative learning tasks needs to be designed. Recently, Pedersen et al. (2017) attempted to combine the drift diffusion and reinforcement learning models. By directly applying the combined model to one learning task, we can expect to gain insight into the relationships between the mathematical parameters. The current study is the first to provide insight into how younger and older adults detect neutral faces that are associated with positive values.

4.1 Implications and future directions

Our findings have theoretical implications. The current results revealed the associations between computational parameters (i.e., learning rate and drift rate) underlying observable behavioral responses during value learning and value-driven detection of neutral faces in young participants. Several previous studies that used computational modeling have shown that the computational parameters reflect latent cognitive processes and are tightly linked to activity in specific brain regions. For example, a recent neuroimaging study reported that the drift rate estimated from face evaluation behaviors using a drift-diffusion model was associated with amygdala activity (Calabro et al., 2023). We expect our findings to provide insights into the neural mechanisms for value-driven detection of neutral faces and their aging patterns, which should be investigated in future computational neuroimaging studies.

Our findings may also have practical implications. A previous study has suggested that computational parameters classified clinical and non-clinical populations better than behavioral measures (Wiecki et al., 2015). A recent study reported that the RT performance of value-driven detection of neutral faces was associated with participants' autistic traits (Saito et al., 2023). Collectively, our findings suggest that the computational modeling of the task may be helpful for the classification of individuals with autism spectrum disorder and those with typical development. Also, because the present study revealed the computational underpinnings of the effect of aging on value learning and value-driven detection of neutral faces, the same approach may provide information about pathological aging, such as dementia (cf. Irwin et al., 2018). Further research is warranted to test the task of value-driven detection of neutral faces and its computational modeling for clinical populations.

4.2 Caveats

This study had several limitations. First, the number of younger participants with successful learning outcomes was greater than that of older participants. The 8:2 feedback ratio used in the associative learning task was difficult for older adults, but may have been too easy for younger adults, thus making it difficult to compare associative learning performance in the visual search task. In the posterior predictive check [Supplementary Figure S1; (see Footnote 2)], the observed data for the older adults who failed to learn had a poor fit with the reinforcement learning model. This also poses a risk of the interpretability of the parameters of reinforcement learning models in the participants who failed to learn. Modification of the feedback ratio in the associative learning task or improving the reinforcement model, which can account for learning failures, is important for future research. The current study compared younger and older participants but factors other than age might contribute the observed differences/relationships. For example, attention is related to intelligence (Schweizer and Moosbrugger, 2004), and it is likely that young participants from Kyoto University and older participants from a local human resource center differ in attributes other than age, such as IQ (Chamorro-Premuzic and Furnham, 2008). The effects of age should be pursued with adequate control of factors that may cause interpretable outcomes. Future studies including older participants should use the Mini-Mental State Examination (Folstein et al., 1975) or other neuropsychological tests to explore whether general cognitive functions are preserved. In addition, the present study applied the diffusion model with a constrained number of trials (i.e., 32), which raises concerns about stable parameter estimates. Even when using only 24 trials, there was a sufficient correlation in the three-parameter diffusion model between the real and predicted values in the systematic simulation (Lerche et al., 2017). Notably, for detecting the condition differences, the noise of parameter estimation might not necessarily be critical. It also holds true that a larger trial count often improves parameter estimation, with the result that future research endeavors may demand the use of more trials and larger sample sizes to enhance the depth and scope of inquiry. Finally, as facial stimuli, the current study used only young male faces with neutral expressions, which may have biased the results considering that male faces tend to be viewed more negatively than female faces (Craig and Lee, 2020). Although emotional recognition performance for the facial expressions of older people is reportedly lower regardless of the observer's age (Riediger et al., 2011), further studies are needed to determine whether this lower performance is applicable to older faces with neutral expressions.

5 Conclusion

In conclusion, we used reinforcement learning and drift diffusion models to compare the value learning process and value-driven detection of neutral faces between younger and older adults. The learning rates in the associative learning task, and the ν and t0 values in the visual search task, were higher in younger than in older participants. Sensitivity to learning feedback may decrease with age. During value-driven detection of neutral faces among young adults, we found that only the sensitivity to reward in the associative learning task promoted efficient accumulation of information during a visual search for neutral faces in younger but not in older adults. The parameter values of our mathematical model shed light on the contributing factors underlying the rapid detection of faces with emotional meaning in younger and older adults. Specifically, the sensitivity to feedback in the associative learning task, the speed of information accumulation and the perceptual time leading to motion onset in the visual search tasks, and the relationship between the speed of information accumulation and feedback sensitivity to reward, decreases with age. The current study underscored the significance of computational modeling in elucidating the cognitive process behind value-driven behavior and contributed to a deeper understanding of aging and related conditions, offering avenues for future investigation and potential interventions in both neuroscience and clinical contexts.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Ethics statement

The studies involving humans were approved by all participants provided written informed consent to take part in the study, which was approved by the ethics committee of the Unit for Advanced

Studies of the Human Mind at Kyoto University and conducted in accordance with institutional ethical guidelines and the Declaration of Helsinki. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

SN: Investigation, Visualization, Writing – original draft, Writing – review & editing. AS: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing – review & editing. WS: Conceptualization, Funding acquisition, Project administration, Supervision, Validation, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was supported by funds from the Japan Science and Technology Agency Core Research for Evolutional Science and Technology (grant number JPMJCR17A5).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2024.1281857/full#supplementary-material

References

Ahn, W. Y., Haines, N., and Zhang, L. (2017). Revealing neurocomputational mechanisms of reinforcement learning and decision-making with the hBayesDM package. *Comput. Psychiatr.* 1, 24–57. doi: 10.1162/CPSY_a_00002

Anderson, B. A., Laurent, P. A., and Yantis, S. (2011). Value-driven attentional capture. *Proc. Natl. Acad. Sci.* 108, 10367–10371. doi: 10.1073/pnas.1104047108

Bürkner, P. C. (2017). Brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80, 1–28. doi: 10.18637/jss.v080.i01

Bürkner, P., Gabry, J., Kay, M., and Vehtari, A. (2023). "Posterior: tools for working with posterior distributions." Available at: https://mc-stan.org/posterior/.

Calabro, R., Lyu, Y., and Leong, Y. C. (2023). Trial-by-trial fluctuations in amygdala activity track motivational enhancement of desirable sensory evidence during perceptual decision-making. *Cereb. Cortex* 33, 5690–5703. doi: 10.1093/cercor/bhac452

Calvo, M. G., and Nummenmaa, L. (2008). Detection of emotional faces: salient physical features guide effective visual search. *J. Exp. Psychol. Gen.* 137, 471–494. doi: 10.1037/a0012771

Chamorro-Premuzic, T., and Furnham, A. (2008). Personality, intelligence and approaches to learning as predictors of academic performance. *Pers. Individ. Differ.* 44, 1596–1603. doi: 10.1016/j.paid.2008.01.003

Cohen, J. (2013). *Statistical power analysis for the behavioral sciences*. New York: Routledge.

Craig, B. M., Becker, S. I., and Lipp, O. V. (2014). Different faces in the crowd: a happiness superiority effect for schematic faces in heterogeneous backgrounds. *Emotion* 14, 794–803. doi: 10.1037/a0036043

Craig, B. M., and Lee, A. J. (2020). Stereotypes and structure in the interaction between facial emotional expression and sex characteristics. *Adapt. Human Behav. Physiol.* 6, 212–235. doi: 10.1007/s40750-020-00141-5

DeCoster, J., Iselin, A. M., and Gallucci, M. (2009). A conceptual and empirical examination of justifications for dichotomization. *Psychol. Methods* 14, 349–366. doi: 10.1037/a0016956

Dombrovski, A. Y., Clark, L., Siegle, G. J., Butters, M. A., Ichikawa, N., Sahakian, B. J., et al. (2010). Reward/punishment reversal learning in older suicide attempters. *Am. J. Psychiatry* 167, 699–707. doi: 10.1176/appi.ajp.2009.09030407

Driver, C. C., and Voelkle, M. C. (2018). Hierarchical bayesian continuous time dynamic modeling. *Psychol. Methods* 23, 774–799. doi: 10.1037/met0000168

Fenske, M. J., and Raymond, J. E. (2006). Affective influences of selective attention. *Curr. Dir. Psychol. Sci.* 15, 312–316. doi: 10.1111/j.1467-8721.2006.00459.x

Folstein, M. F., Folstein, S. E., and McHugh, P. R. (1975). "Mini-mental state": a practical method for grading the cognitive state of patients for the clinician. *J. Psychiatr. Res.* 12, 189–198. doi: 10.1016/0022-3956(75)90026-6

Forstmann, B. U., Ratcliff, R., and Wagenmakers, E. J. (2016). Sequential sampling models in cognitive neuroscience: advantages, applications, and extensions. *Annu. Rev. Psychol.* 67, 641–666. doi: 10.1146/annurev-psych-122414-033645

Gabry, J., Češnovar, R., and Johnson, A. (2023). Cmdstanr: R interface to 'CmdStan'. Available at: https://mc-stan.org/cmdstanr/, https://discourse.mc-stan.org.

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., and Gelman, A. (2019). Visualization in Bayesian workflow. *J. R. Stat. Soc. Ser. A Stat. Soc.* 182, 389–402. doi: 10.1111/rssa.12378

Gelman, A., and Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge university press.

Hansen, C. H., and Hansen, R. D. (1988). Finding the face in the crowd: an anger superiority effect. *J. Pers. Soc. Psychol.* 54, 917–924. doi: 10.1037/0022-3514.54.6.917

Heerdink, M. W., van Kleef, G. A., Homan, A. C., and Fischer, A. H. (2015). Emotional expressions as social signals of rejection and acceptance: evidence from the affect misattribution paradigm. *J. Exp. Soc. Psychol.* 56, 60–68. doi: 10.1016/j.jesp.2014.09.004

Hertwig, R., Barron, G., Weber, E. U., and Erev, I. (2004). Decisions from experience and the effect of rare events in risky choice. *Psychol. Sci.* 15, 534–539. doi: 10.1111/j.0956-7976.2004.00715.x

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6, 65–70,

Horstmann, G., Borgstedt, K., and Heumann, M. (2006). Flanker effects with faces may depend on perceptual as well as emotional differences. *Emotion* 6, 28–39. doi: 10.1037/1528-3542.6.1.28

Horstmann, G., Lipp, O. V., and Becker, S. I. (2012). Of toothy grins and angry snarls—open mouth displays contribute to efficiency gains in search for emotional faces. *J. Vis.* 12:7. doi: 10.1167/12.5.7

Irwin, K., Sexton, C., Daniel, T., Lawlor, B., and Naci, L. (2018). Healthy aging and dementia: two roads diverging in midlife? *Front. Aging Neurosci.* 10:275. doi: 10.3389/fnagi.2018.00275

Iseki, R. (2023). Anovakun version 4.8.9. Available at: http://riseki.php.xdomain.jp/index.php?ANOVA%E5%90%9B

Kaelbling, L. P., Littman, M. L., and Moore, A. W. (1996). Reinforcement learning: a survey. *J. Artif. Intell. Res.* 4, 237–285. doi: 10.1613/jair.301

Kahneman, D., and Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–292. doi: 10.2307/1914185

Katahira, K. (2015). The relation between reinforcement learning parameters and the influence of reinforcement history on choice behavior. *J. Math. Psychol.* 66, 59–69. doi: 10.1016/j.jmp.2015.03.006

Katahira, K., Fujimura, T., Okanoya, K., and Okada, M. (2011). Decision-making based on emotional images. *Front. Psychol.* 2:311. doi: 10.3389/fpsyg.2011.00311

Kinosada, Y. (2019). Compare parameters across conditions for within-participant factors in the experiment (in Japanese). Available at: https://das-kino.hatenablog.com/entry/2019/12/22/222333

Kwak, Y., Pearson, J., and Huettel, S. A. (2014). Differential reward learning for self and others predicts self-reported altruism. *PLoS One* 9:e107621. doi: 10.1371/journal.pone.0107621

Lee, M. D., and Wagenmakers, E.-J. (2014). *Bayesian cognitive modeling: a practical course*. Cambridge, UK: Cambridge University Press.

Lerche, V., Voss, A., and Nagler, M. (2017). How many trials are required for parameter estimation in diffusion modeling? A comparison of different optimization criteria. *Behav. Res. Methods* 49, 513–537. doi: 10.3758/s13428-016-0740-2

Mill, A., Allik, J., Realo, A., and Valk, R. (2009). Age-related differences in emotion recognition ability: a cross-sectional study. *Emotion* 9, 619–630. doi: 10.1037/a0016562

Muller, S., Rothermund, K., and Wentura, D. (2016). Relevance drives attention: attentional bias for gain-and loss-related stimuli is driven by delayed disengagement. *Q. J. Exp. Psychol.* 69, 752–763. doi: 10.1080/17470218.2015.1049624

Namba, S., Sato, W., Nakamura, K., and Watanabe, K. (2022). Computational process of sharing emotion: an authentic information perspective. *Front. Psychol.* 13:849499. doi: 10.3389/fpsyg.2022.849499

Pedersen, M. L., Frank, M. J., and Biele, G. (2017). The drift diffusion model as the choice rule in reinforcement learning. *Psychon. Bull. Rev.* 24, 1234–1251. doi: 10.3758/s13423-016-1199-y

Puls, S., and Rothermund, K. (2018). Attending to emotional expressions: no evidence for automatic capture in the dot-probe task. *Cogn. Emot.* 32, 450–463. doi: 10.1080/02699931.2017.1314932

R Core Team (2019). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ratcliff, R. (1978). A theory of memory retrieval. *Psychol. Rev.* 85, 59–108. doi: 10.1037/0033-295X.85.2.59

Ratcliff, R., and McKoon, G. (2008). The diffusion decision model: theory and data for two-choice decision tasks. *Neural Comput.* 20, 873–922. doi: 10.1162/neco.2008.12-06-420

Ratcliff, R., and Rouder, J. N. (1998). Modeling response times for two-choice decisions. *Psychol. Sci.* 9, 347–356. doi: 10.1111/1467-9280.00067

Reed, A. E., Chan, L., and Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: age differences in preferences for positive over negative information. *Psychol. Aging* 29, 1–15. doi: 10.1037/a0035194

Reinhart, A. (2015). *Statistics done wrong: the woefully complete guide*. San Francisco, CA: No Starch Press.

Rescorla, R. A., and Wagner, A. R. (1972). "A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement" in *Classical conditioning II: current research and theory*. eds. A. H. Black and W. F. Prokasy (New York: Appleton-Century-Crofts).

Richoz, A. R., Lao, J., Pascalis, O., and Caldara, R. (2018). Tracking the recognition of static and dynamic facial expressions of emotion across the life span. *J. Vis.* 18:5. doi: 10.1167/18.9.5

Riediger, M., Voelkle, M. C., Ebner, N. C., and Lindenberger, U. (2011). Beyond "happy, angry, or sad?": age-of-poser and age-of-rater effects on multi-dimensional emotion perception. *Cogn. Emot.* 25, 968–982. doi: 10.1080/02699931.2010.540812

Saito, A., Sato, W., and Yoshikawa, S. (2020). Older adults detect happy facial expressions less rapidly. *R. Soc. Open Sci.* 7:191715. doi: 10.1098/rsos.191715

Saito, A., Sato, W., and Yoshikawa, S. (2022a). Rapid detection of neutral faces associated with emotional value among older adults. *J. Gerontol. B Psychol. Sci. Soc. Sci.* 77, 1219–1228. doi: 10.1093/geronb/gbac009

Saito, A., Sato, W., and Yoshikawa, S. (2022b). Rapid detection of neutral faces associated with emotional value. *Cogn. Emot.* 36, 546–559. doi: 10.1080/02699931.2021.2017263

Saito, A., Sato, W., and Yoshikawa, S. (2023). Brief research report: autistic traits modulate the rapid detection of punishment-associated neutral faces. *Front. Psychol.* 14:1284739. doi: 10.3389/fpsyg.2023.1284739

Salthouse, T. A. (2000). Aging and measures of processing speed. *Biol. Psychol.* 54, 35–54. doi: 10.1016/S0301-0511(00)00052-1

Sato, W., Hyniewska, S., Minemoto, K., and Yoshikawa, S. (2019). Facial expressions of basic emotions in japanese laypeople. *Front. Psychol.* 10:259. doi: 10.3389/fpsyg.2019.00259

Sawada, R., Sato, W., Nakashima, R., and Kumada, T. (2022). How are emotional facial expressions detected rapidly and accurately? A diffusion model analysis. *Cognition* 229:105235. doi: 10.1016/j.cognition.2022.105235

Schweizer, K., and Moosbrugger, H. (2004). Attention and working memory as predictors of intelligence. *Intelligence* 32, 329–347. doi: 10.1016/j.intell.2004.06.006

Stan Development Team. (2020). Stan modeling language users guide and reference manual, version 2.21.2. Available at: https://mc-stan.org

Stins, J. F., Roelofs, K., Villain, J., Kooijman, K., Hagenaars, M. A., and Beek, P. J. (2011). Walk to me when I smile, step back when I'm angry: emotional faces modulate whole-body approach–avoidance behaviors. *Exp. Brain Res.* 212, 603–611. doi: 10.1007/s00221-011-2767-z

Suzuki, S., Zhang, X., Dezfouli, A., Braganza, L., Fulcher, B. D., Parkes, L., et al. (2023). Individuals with problem gambling and obsessive-compulsive disorder learn through distinct reinforcement mechanisms. *PLoS Biol.* 21:e3002031. doi: 10.1371/journal.pbio.3002031

Tannert, S., and Rothermund, K. (2020). Attending to emotional faces in the flanker task: probably much less automatic than previously assumed. *Emotion* 20, 217–235. doi: 10.1037/emo0000538

Tipples, J. (2019). Recognising and reacting to angry and happy facial expressions: a diffusion model analysis. *Psychol. Res.* 83, 37–47. doi: 10.1007/s00426-018-1092-6

Wentura, D., Muller, P., and Rothermund, K. (2014). Attentional capture by evaluative stimuli: gain-and loss-connoting colors boost the additional-singleton effect. *Psychon. Bull. Rev.* 21, 701–707. doi: 10.3758/s13423-013-0531-z

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D. A., François, R., et al. (2019). Welcome to the Tidyverse. *J. Open Source Softw.* 4:1686. doi: 10.21105/joss.01686

Wiecki, T. V., Poland, J., and Frank, M. J. (2015). Model-based cognitive neuroscience approaches to computational psychiatry: clustering and classification. *Clin. Psychol. Sci.* 3, 378–399. doi: 10.1177/2167702614565359

Zhao, M.-F., Zimmer, H. D., Shen, X., Chen, W., and Fu, X. (2016). Exploring the cognitive processes causing the age-related categorization deficit in the recognition of facial expressions. *Exp. Aging Res.* 42, 348–364. doi: 10.1080/0361073X.2016.1191854

Ziaei, M., and Fischer, H. (2016). "Emotion and aging: the impact of emotion on attention, memory, and face recognition in late adulthood" in *Neuroimaging personality, social cognition, and character*. eds. J. R. Absher and J. Cloutier (Cambridge, MA: Elsevier Academic Press), 259–278.

frontiers | Frontiers in Psychology

TYPE Opinion
PUBLISHED 30 May 2024
DOI 10.3389/fpsyg.2024.1347890

OPEN ACCESS

EDITED BY
Florin Dolcos,
University of Illinois at Urbana-Champaign,
United States

REVIEWED BY
Annisa Ristya Rahmanti,
Gadjah Mada University, Indonesia

*CORRESPONDENCE
Alexander Tagesson
✉ alexander.tagesson@lucs.lu.se

RECEIVED 04 December 2023
ACCEPTED 15 May 2024
PUBLISHED 30 May 2024

CITATION
Tagesson A and Stenseke J (2024) Do you feel like (A)I feel? *Front. Psychol.* 15:1347890.
doi: 10.3389/fpsyg.2024.1347890

Do you feel like (A)I feel?

Alexander Tagesson* and Jakob Stenseke

Department of Philosophy, Lund University, Lund, Sweden

KEYWORDS

empathy, emotion, artificial intelligence (AI), perspective-taking, experience sharing

Most of us are familiar with the uncomfortable feeling that results from skepticism about others' capacity to see the world as we do. If we dig too deep into this solipsistic worry, we might feel alone in the universe—*no one can feel what it is like to be me*. One might say that it is a question of attitude. Regardless of whether the other actually *can* empathize with us, our attitude prevents us from believing it. In a correspondence article in *Nature Human Behaviour*, Perry (2023) recently made her attitude toward the prospect of empathic AI clear: they will never know how it feels to be human! This sentiment is part of a broader aversion toward the prospect of artificial empathy (AE) (e.g., Montemayor et al., 2022; Zaki, 2023). While we agree that these dystopic concerns should be taken seriously, we also believe that the debate would benefit from additional nuance. More precisely, we argue that the AI systems of today—exemplified by AE skeptics such as Perry—are not the appropriate metric to evaluate the potential for AE and should not be used as support for why people might dismiss AE as non-genuine empathy.

At the core of Perry's critique is the observation that AE is well-received until recipients realize it was generated by an AI. Perry provides two explanations for this "artificial-empathy paradox". Firstly, "AI can learn to say the right words—but knowing that AI generated them demolishes any potential for sensing that one's pain or joy is genuinely being shared". Secondly, human empathy is valued *because* it is demanding and finite, and since "AI entails no emotional or time cost", it fails to indicate that "the recipient holds any unique importance". However, we argue that neither explanation succeeds in discrediting the prospect of artificial empathy.

Empathy is a notoriously convoluted concept (see Cuff et al., 2016 for a review) and researchers often highlight cognitive-, affective-, and motivational components of empathy (Zaki, 2014; Perry, 2023). Cognitive empathy, sometimes called perspective-taking or mentalizing, is the intellectual ability to understand how the other perceives and experiences their situation (Decety and Cowell, 2014; Zaki and Ochsner, 2016; Marsh, 2018). Cognitive empathy is to a degree already achievable for AI, which can detect and identify human emotions (Montemayor et al., 2022; Perry, 2023). Affective empathy, or experience sharing, refers to how one vicariously feels and experiences the other's emotional states (Decety and Cowell, 2014; Zaki and Ochsner, 2016; Marsh, 2018). This kind of experience-sharing is potentially not obtainable for AI. Lacking lived subjective experience (Montemayor et al., 2022; Perry, 2023), trying to share the experience of an emotional human may not resonate adequately as the AI reasonably does not feel anything (Turkle, 2007). The motivational component, also called empathic concern, can be understood as a motivation to support others' wellbeing or help them alleviate suffering (Decety and Cowell, 2014; Zaki and Ochsner, 2016; Marsh, 2018). However, while it is reasonable to contest the extent to which AI can manifest affective empathy and empathic concern, we disagree with the argument that it comes down to the human recipients' attitude toward AE (Montemayor et al., 2022; Perry, 2023).

Whether empathy is valuable is *not* (solely) a question of the recipient's attitude toward the empathizer. The value of the empathy a parent directs toward her child cannot easily be discarded based on whether the child takes the parent to be a genuine empathizer or not. Similarly, the fact that some foster negative attitudes toward psychologists, which prevents them from seeking therapy that would be beneficial for them, does not discredit the value of therapy. If we view empathy as a question of attitude, then we are exposed to the solipsistic worry: what prevents us from having the "wrong" attitude toward genuine empathizers? Perry merely assumes the anthropocentric standard view: only human activities are valuable for humans (Singer, 1975). This view is also prevalent in our attitudes toward animals. Studies show that people's tendency to not attribute mental capabilities (e.g., empathy) to animals fails to live up to their own self-reported normative standards (Leach et al., 2023). This effect was attenuated when ascribing a mind and mental capabilities to humans, displaying another example of anthropocentrism. Fortunately, attitudes can change, and if it is our attitudes toward animals and AIs that are decisive for granting them genuine empathy, couldn't they also change? In another recent study, researchers manipulated participants' attitudes toward AI, making them believe that the algorithm either had a manipulative motive, a caring motive, or no particular motive. This considerably changed how participants perceived and interacted with the AI, where participants in the care motive-, or empathic concern-, group perceived it as more empathetic than participants in the two other groups. Notably, the effect was stronger for more sophisticated AI (Pataranutaporn et al., 2023). These results suggest that our attitudes and the technological sophistication of the algorithm had an impact on participants' perception of AI as being empathetic. Consequently, we believe that our malleable attitudes toward AI, combined with increased technological sophistication, will impact our perception of AE, making it more likely to be perceived as genuine empathy. Furthermore, we are also not convinced by Perry's claim that because human empathy is demanding and limited, choosing to empathize communicates the importance of the recipient to the empathizer. A recent study showed that when people learned that empathy is an unlimited resource, they became more empathic, with real-life consequences, e.g., more likely to hug an out-group member (Hasson et al., 2022). These recipients of empathy and hugs would likely not deem the empathy they received as less genuine if they learned that the empathizer believed empathy to be unlimited and not finite, which led them to feel and behave more empathically.

AI already displays cognitive empathic abilities and is capable of generating generic empathic responses. Due to vast advancements in computational approaches to emotional inference, AI has demonstrated the ability to identify human emotions (Ong et al., 2019), manifest facial emotions (Mishra et al., 2023), and to successfully facilitate empathetic interactions (Ayers et al., 2023; Sharma et al., 2023). For instance, a recent example showed how human-AI collaboration produced more empathic conversations in peer-to-peer mental health support in comparison to human-only responses (Sharma et al., 2023). In another case, healthcare professionals found AI's responses to medical questions to be almost ten times as empathetic as the responses from human physicians (Ayers et al., 2023). These generic applications of empathic displays are impressive, but when recipients learn that the empathy they received is AI-generated, they will likely not perceive it as genuine empathy. As Perry points out, "AI empathy fails to convey authentic care or to indicate that the recipient holds any unique importance". This might not be surprising as these examples merely attest to AI's capability of emotion detection and empathic signaling and are designed to respond empathetically to anyone repeatedly. In contrast, the motivated nature of human empathy often leads people to empathize in discriminating ways (Zaki, 2014; Bloom, 2016) and with few people (Cameron and Payne, 2011; Cameron et al., 2022). Thus, generic AI applications not only deprive recipients of the feeling of uniqueness; their empathic displays are also dissimilar to how humans empathize, making them seem non-genuine. The real test of artificial empathy—by Perry's own standards—would be through personalized algorithms tuned to their human. We can envision algorithms that respond with enthusiasm and authentic care to their particular person, making *that* person more important than any other. As the relationships deepen, the personalized algorithm will be able to display more empathy toward its person, paralleling how empathy is extended in humans (Depow et al., 2021). Recipients of this kind of AE will likely perceive the care as authentic and the concern as genuine, as there are already examples of people developing strong feelings for their AI companions (Pentina et al., 2023).

While we take issue with Perry's view, we also acknowledge that much more needs to be said about the potential value and risks of AE. For instance, several ethical issues need to be seriously addressed for the responsible development and deployment of AE, e.g., regarding privacy (Lutz et al., 2019), deception (Park et al., 2023), and negative impacts on human-human relationships (Turkle, 2010). A lot more can also be said about the potential benefits of AE; e.g., how it may alleviate many of the problems associated with human empathy, such as biases, e.g., ingroup empathy bias (Cikara et al., 2014) or compassion fade (Västfjäll et al., 2014). It could potentially also lessen some of the taxing costs associated with empathy (Cameron et al., 2019) and reduce compassion fatigue (Cocker and Joss, 2016) on the part of human empathizers. To this end, researchers have called for strategic regulations of different components of empathy, i.e., affective-, cognitive- and motivational-, to attain critical outcomes (Weisz and Cikara, 2021). Similarly, we could strategically apply different components of AE to enhance human flourishing. While all these considerations must be weighed against each other to determine the overall risk-benefit of AE, contrary to what Perry claims, human attitudes toward AI do not seem to present an insurmountable obstacle.

In sum, Perry's criticism of the value of artificial empathy seems unjustified. It might turn out to be the case that full-fledged AE is unobtainable due to principled obstacles for AI to simulate human empathy. Those are other, more legitimate, reasons for not granting AI empathy than due to recipients' changeable attitudes about AE. Before making any conclusive remarks about AE being perceived as genuine empathy or not, we need to create and evaluate AI applications that better emulate human empathy. It is possible that these applications may change our attitudes so that we start perceiving artificial empathy, or parts of it, as genuine empathy.

Author contributions

AT: Writing – original draft, Writing – review & editing. JS: Writing – original draft, Writing – review & editing.

Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Ayers, J. W., Poliak, A., Dredze, M., Leas, E. C., Zhu, Z., Kelley, J. B., et al. (2023). Comparing physician and artificial intelligence chatbot responses to patient questions posted to a public social media forum. *JAMA Intern. Med.* 183, 589–596. doi: 10.1001/jamainternmed.2023.1838

Bloom, P. (2016). *Against Empathy: The Case for Rational Compassion.* New York, NY: Ecco.

Cameron, C. D., Hutcherson, C. A., Ferguson, A. M., Scheffer, J. A., Hadjiandreou, E., Inzlicht, M., et al. (2019). Empathy is hard work: people choose to avoid empathy because of its cognitive costs. *J. Exp. Psychol. General* 148, 962–976. doi: 10.1037/xge0000595

Cameron, C. D., and Payne, B. K. (2011). Escaping affect: how motivated emotion regulation creates insensitivity to mass suffering. *J. Pers. Soc. Psychol.* 100, 1–15. doi: 10.1037/a0021643

Cameron, C. D., Scheffer, J. A., Hadjiandreou, E., and Anderson, S. (2022). Chapter four - motivated empathic choices. *Adv. Exp. Soc. Psychol.* 66, 191–279. doi: 10.1016/bs.aesp.2022.04.005

Cikara, M., Bruneau, E., Van Bavel, J. J., and Saxe, R. (2014). Their pain gives us pleasure: how intergroup dynamics shape empathic failures and counter-empathic responses. *J. Exp. Soc. Psychol.* 55, 110–125. doi: 10.1016/j.jesp.2014.06.007

Cocker, F., and Joss, N. (2016). Compassion fatigue among healthcare, emergency and community service workers: a systematic review. *Int. J. Environ. Res. Public Health.* 13:618. doi: 10.3390/ijerph13060618

Cuff, B. M. P., Brown, S. J., Taylor, L., and Howat, D. J. (2016). Empathy: a review of the concept. *Emot. Rev.* 8, 144–153. doi: 10.1177/1754073914558466

Decety, J., and Cowell, J. M. (2014). The complex relation between morality and empathy. *Trends Cogn. Sci.* 18, 337–339. doi: 10.1016/j.tics.2014.04.008

Depow, G. J., Francis, Z., and Inzlicht, M. (2021). The experience of empathy in everyday life. *Psychol. Sci.* 32, 1198–1213. doi: 10.1177/0956797621995202

Hasson, Y., Amir, E., Sobol-Sarag, D., Tamir, M., and Halperin, E. (2022). Using performance art to promote intergroup prosociality by cultivating the belief that empathy is unlimited. *Nat. Commun.* 13:7786. doi: 10.1038/s41467-022-35235-z

Leach, S., Sutton, R. M., Dhont, K., Douglas, K. M., and Bergström, Z. M. (2023). Changing minds about minds: Evidence that people are too sceptical about animal sentience. *Cognition* 230:105263. doi: 10.1016/j.cognition.2022.105263

Lutz, C., Schöttler, M., and Hoffmann, C. P. (2019). The privacy implications of social robots: scoping review and expert interviews. *Mobile Media Commun.* 7, 412–434. doi: 10.1177/2050157919843961

Marsh, A. A. (2018). The neuroscience of empathy. *Curr. Opin. Behav. Sci.* 19, 110–115. doi: 10.1016/j.cobeha.2017.12.016

Mishra, C., Verdonschot, R., Hagoort, P., and Skantze, G. (2023). Real-time emotion generation in human-robot dialogue using large language models. *Front. Robot. AI* 10:1271610. doi: 10.3389/frobt.2023.1271610

Montemayor, C., Halpern, J., and Fairweather, A. (2022). In principle obstacles for empathic AI: why we can't replace human empathy in healthcare. *AI Soc.* 37, 1353–1359. doi: 10.1007/s00146-021-01230-z

Ong, D. C., Zaki, J., and Goodman, N. D. (2019). Computational models of emotion inference in theory of mind: a review and roadmap. *Top. Cogn. Sci.* 11, 338–357. doi: 10.1111/tops.12371

Park, P. S., Goldstein, S., O'Gara, A., Chen, M., and Hendrycks, D. (2023). AI deception: a survey of examples, risks, and potential solutions. *ArXiv* [preprint]. *abs/2308.14752.*

Pataranutaporn, P., Liu, R., Finn, E., and Maes, P. (2023). Influencing human–AI interaction by priming beliefs about AI can increase perceived trustworthiness, empathy and effectiveness. *Nat. Mach. Intell.* 5, 1076–1086. doi: 10.1038/s42256-023-00720-7

Pentina, I., Hancock, T., and Xie, T. (2023). Exploring relationship development with social chatbots: a mixed-method study of replika. *Comput. Human Behav.* 140:107600. doi: 10.1016/j.chb.2022.107600

Perry, A. (2023). AI will never convey the essence of human empathy. *Nat Hum Behav*. 7, 1808–9. doi: 10.1038/s41562-023-01675-w

Sharma, A., Lin, I. W., Miner, A. S., Atkins, D. C., and Althoff, T. (2023). Human–AI collaboration enables more empathic conversations in text-based peer-to-peer mental health support. *Nat. Mach. Intell.* 5, 46–57. doi: 10.1038/s42256-022-00593-2

Singer, P. (1975). *Animal Liberation: A New Ethics for Our Treatment of Animals.* New York, NY: The New York Review.

Turkle, S. (2007). Authenticity in the age of digital companions. *Interact. Stud.* 8, 501–517. doi: 10.1075/is.8.3.11tur

Turkle, S. (2010). "In good company? On the threshold of robotic companions," in *Close Engagements With Artificial Companions: Key Social, Psychological, Ethical and Design Issues*, ed. Y. Wilks (Amsterdam: John Benjamins Publishing), 3–10.

Västfjäll, D., Slovic, P., Mayorga, M., and Peters, E. (2014). Compassion fade: affect and charity are greatest for a single child in need. *PLoS ONE* 9:e100115. doi: 10.1371/journal.pone.0100115

Weisz, E., and Cikara, M. (2021). Strategic regulation of empathy. *Trends Cogn. Sci.* 25, 213–227. doi: 10.1016/j.tics.2020.12.002

Zaki, J. (2014). Empathy: a motivated account. *Psychol. Bull.* 140, 1608–1647. doi: 10.1037/a0037679

Zaki, J. (2023). *How Artificial Empathy Will Change Work and Life, According to a Stanford Professor.* The Future of Work. Available online at: https://www.fastcompany.com/90984653/how-artificial-empathy-will-impact-workers-and-customers-according-to-a-stanford-professor (accessed February 08, 2024).

Zaki, J., and Ochsner, K. N. (2016). "Empathy," in *Handbook of Emotion, 4th Edn*, eds. L. Feldman-Barrett, M. Lewis, and J. M. Haviland-Jones (New York, NY: Guilford Press), 871–884.

frontiers | Frontiers in Psychology

TYPE Original Research
PUBLISHED 30 December 2024
DOI 10.3389/fpsyg.2024.1459617

OPEN ACCESS

EDITED BY
Michiko Sakaki,
University of Tübingen, Germany

REVIEWED BY
Valerio Santangelo,
University of Perugia, Italy
Marco Costanzi,
Libera Università Maria SS. Assunta, Italy

*CORRESPONDENCE
Carlos Ventura-Bort
✉ ventura@uni-potsdam.de
Mathias Weymar
✉ mathias.weymar@uni-potsdam.de

RECEIVED 04 July 2024
ACCEPTED 10 December 2024
PUBLISHED 30 December 2024

CITATION
Ventura-Bort C, Katsumi Y, Wirkner J, Wendt J, Schwabe L, Hamm AO, Dolcos F and Weymar M (2024) Disentangling emotional source memory: a mega-analysis on the effects of emotion on item-context binding in episodic long-term memory.
Front. Psychol. 15:1459617.
doi: 10.3389/fpsyg.2024.1459617

Disentangling emotional source memory: a mega-analysis on the effects of emotion on item-context binding in episodic long-term memory

Carlos Ventura-Bort[1]*, Yuta Katsumi[2], Janine Wirkner[3], Julia Wendt[1], Lars Schwabe[4], Alfons O. Hamm[3], Florin Dolcos[5] and Mathias Weymar[1,6]*

[1]Department of Biological Psychology and Affective Science, Faculty of Human Sciences, University of Potsdam, Potsdam, Germany, [2]Department of Neurology, Massachusetts General Hospital and Harvard Medical School, Boston, MA, United States, [3]Department of Clinical Psychology and Psychotherapy, Institute of Psychology, University of Greifswald, Greifswald, Germany, [4]Department of Cognitive Psychology, Institute of Psychology, Universität Hamburg, Hamburg, Germany, [5]Department of Psychology, Neuroscience Program, Beckman Institute for Advanced Science and Technology, University of Illinois Urbana-Champaign, Urbana, IL, United States, [6]Faculty of Health Sciences Brandenburg, University of Potsdam, Potsdam, Germany

Introduction: It has long been known that highly arousing emotional single items are better recollected than low arousing neutral items. Despite the robustness of this memory advantage, emotional arousing events may not always promote the retrieval of source details (i.e., source memory) or associated neutral information.

Methods: To shed more light on these effects, we pooled data from seven different studies ($N = 333$) to investigate the role of emotion on item-context binding in episodic memory, as well as potential interacting factors (e.g., encoding instructions, type of retrieval task, or acute stress). In all studies, participants incidentally encoded common neutral objects (i.e., items), overlaid on different pleasant, neutral, or unpleasant background scenes (i.e., contexts). One week later, the encoded objects were presented intermixed with new ones and memory for item and source contextual details was tested, also considering the contribution of recollection and familiarity-based processes.

Results: Linear mixed models revealed a recollection-based retrieval advantage for unpleasant and pleasant source contextual details compared to neutral ones. Bayes hypothesis-testing analysis further indicated decisive evidence in favor of a relevant role of emotional arousal and recollection in source contextual memory. Regarding item memory, linear mixed models revealed enhanced recollection-based memory for items encoded in pleasant contexts compared to their neutral and unpleasant counterparts. However, Bayes analysis revealed strong to moderate evidence for models without affective category (or its interactions), indicating that the affective category of contexts in which objects were paired during encoding had little influence on item memory performance.

Discussion: The present results are discussed in relation to existing evidence and current neurobiological models of emotional episodic memory by also emphasizing the role of predictive processing as a useful conceptual framework to understand the effects of emotion on memory for source details and associated neutral information.

KEYWORDS

emotion, episodic memory, long-term memory, source memory, mega-analysis

Introduction

Whereas, most everyday experiences remain in our memory for only a few moments, highly arousing (i.e., pleasant and unpleasant) events such as the first bike ride, a wedding, or an injuring car accident may accompany us forever, as if they "almost left a scar in our cerebral tissue" (cf. James, 1890). Empirical evidence has well established the memory advantage for highly arousing single items (Bradley et al., 1992; Dolcos et al., 2005, 2017, 2020; Schiller et al., 2023; Weymar et al., 2009, 2011; Weymar and Hamm, 2013; Williams et al., 2022). This affective enhancement of memory is less associated with a familiarity-based (i.e., retrieval of an event without specifics) and more with a recollection-based experience (i.e., an elaborate process that includes the retrieval of specific details of the encoding event; Dolcos et al., 2005; Weymar and Hamm, 2013). In real-world situations, however, single items are rarely encountered in isolation, but are rather temporally dynamic (Palombo and Cocquyt, 2020; Bogdan et al., 2023), encoded with other information (Ranganath, 2010), and embedded in a particular context (Chiu et al., 2013). One question, thus, arises as to whether emotion also enhances the retrieval of details that are part of the emotional event (e.g., the *how*, *when*, or *where*, and associated neutral information)—i.e., *source* memory (Chiu et al., 2013; Dolcos et al., 2017; Mather and Sutherland, 2011; Mather et al., 2016; Murray and Kensinger, 2013; Squire et al., 2007). Available evidence suggests that despite the robustness of the memory enhancing effects of emotion on single items, affectively-laden information may sometimes *enhance* (D'Argembeau and Van der Linden, 2005; Doerksen and Shimamura, 2001; Graciela et al., 2016; Guillet and Arndt, 2009; Henson et al., 2016; Luck et al., 2014; Maratos and Rugg, 2001; Mather et al., 2009; Mather and Knight, 2008; Minor and Herzmann, 2019; Nashiro and Mather, 2011; Rimmele et al., 2012; Smith et al., 2004, 2005; Ventura-Bort et al., 2016a,b) or *impair* (Bisby et al., 2015; Bisby and Burgess, 2014; Cook et al., 2007; Ferré et al., 2019; Guo et al., 2018; Kensinger et al., 2007; MacKenzie et al., 2015; Madan et al., 2017, 2012; Mao et al., 2015; Mather et al., 2006, 2009; Mather and Knight, 2008; Nashiro and Mather, 2011; Rimmele et al., 2011; Touryan et al., 2007) the retrieval of source details (e.g., colors, spatial location, contexts, and temporal order of presentation) and associated neutral material (e.g., objects, words). These heterogeneous findings related to the effects of emotion on item-context binding in episodic source memory may be due to various factors (Mather et al., 2016; Bogdan et al., 2024), of which we consider the following two as critical: (1) the *prioritization* that the to-be-retrieved information receives and (2) the *retention interval* between encoding and retrieval.

According to the Arousal-Biased Competition (ABC) Theory (Mather and Sutherland, 2011), the modulatory effects of emotion on memory details depend upon the attentional priority that the critical information receives during encoding (e.g., via bottom-up perceptual salience, top-down attentional focus, or prior experience with particular stimuli). Emotion can enhance memory for source details or associated neutral items if they are highly prioritized, integrated in, or unitized with affective information, and can impair it if less prioritized or perceived as a competitor for resources against affective information (Mather et al., 2016; Mather and Sutherland, 2011). Neurobiological mechanisms for these opposing effects have been proposed in the *glutamate amplifies noradrenergic effects* (GANE) model (Mather et al., 2016). The GANE model suggests that prioritization of information occurs as a result of positive (or negative) feedback between glutamatergic neurons and noradrenergic varicosities of the locus coeruleus (LC) that potentiates (or diminishes) the neuronal activation associated with the mental representation of the prioritized (or non-prioritized) information. Importantly, the LC has widespread projections to brain regions that are thought to modulate encoding and consolidation of emotionally relevant information, including the hippocampus (e.g., Harley, 2007; Mello-Carpes and Izquierdo, 2013) and the amygdala (e.g., Chen and Sara, 2007; Clayton and Williams, 2000; McIntyre et al., 2012; Ventura-Bort et al., 2021; Williams et al., 1998), which are tightly linked to affective episodic memory (Dolcos et al., 2004, 2005, 2017; LaBar and Cabeza, 2006). It has, thus, been proposed that the enhancing effects of prioritization on source details or neutral items encoded with highly arousing information is supported by a positive interaction between glutamate and noradrenaline (NA) in these memory-sensitive regions (Mather et al., 2016).

In parallel to the fast, central phasic noradrenergic release that occurs after the encoding of affectively relevant information, slower physiological responses are initiated, resulting in the release of adrenal stress hormones (epinephrine and glucocorticoids). This peripheral hormonal release modulates central NA and corticosteroids levels in the amygdala and hippocampus (Henckens et al., 2009; McGaugh, 2000, 2004; McIntyre et al., 2012; Schwabe, 2017; Schwabe et al., 2022; Strange and Dolan, 2004), exerting special influence on memory consolidation processes (McGaugh, 2004; McIntyre et al., 2012; Schwabe et al., 2013; Strange and Dolan, 2004). Indeed, when memory for emotional and neutral items is tested after short retention intervals (e.g., 3–5 min after encoding)—diminishing the influence of peripheral catecholamines and glucocorticoids release in modulating central activity—, the recognition advantage for highly arousing vs. neutral items is less pronounced (Sharot et al., 2004; Sharot and Yonelinas, 2008; Schümann et al., 2017) compared to when tested after longer retention intervals (>24 h; Dolcos et al., 2005; Ritchey et al., 2008; Schümann et al., 2017; Segal and Cahill, 2009; Sharot et al., 2004; Sharot and Yonelinas, 2008; Weymar et al., 2009, 2010). These effects that may be mediated by enhanced consolidation processes may further extend to source memory retrieval as a memory advantage for source details paired with highly arousing (particularly unpleasant) compared with non-arousing information, has been found after long, but not short, retention intervals (Pierce and Kensinger, 2011).

Under the assumptions that high prioritization and long retention intervals may boost the impact of emotion on source memory and associated neutral items, we investigated—across a series of studies—their effect on emotional item-context binding on behavioral and neural level (Ventura-Bort et al., 2016a,b, 2020b, 2024 see also Table 1 for unpublished studies). In the first session, participants incidentally encoded common neutral objects (i.e., items), overlaid on different pleasant, neutral, or unpleasant background scenes (i.e., contexts). Later, the encoded objects were presented intermixed with new ones and memory for items and source contextual details were assessed.[1] Critically, high prioritization was promoted by presenting the neutral objects prior to the scenes to ensure that they capture attentional resources. In addition, to facilitate the item-context binding, objects were not visually separated from the background scenes (Jaeger et al., 2009; Jaeger and Rugg, 2012; Smith et al., 2004, 2005), but directly overlaid on top of them. In addition, most studies included an encoding instruction to imagine the object as a part of the scene further facilitate item-context binding (Ventura-Bort et al., 2016a). Furthermore, we used a long retention interval (i.e., 1 week) to promote consolidation processes. To differentiate between familiarity and recollection processes we further used the Remember/Know procedure (Tulving, 1985) in most of the studies. In this task, participants indicate whether they can retrieve rich contextual details of the contiguous attributes of the encoding episode (i.e., Remember judgments), a process associated with recollection, or whether their retrieval lacks contextual specifics (i.e., Know judgments), a phenomenon associated with familiarity. Across studies, we observed consistent recollection-driven source memory enhancement for highly arousing source contextual information, but the expected memory advantage for items integrated in pleasant and unpleasant contexts was less reliable (e.g., Ventura-Bort et al., 2020b, 2024). In some cases, the memory advantage for objects from both pleasant and unpleasant contexts was observed (Ventura-Bort et al., 2020a), in others, these effects were exclusively found for items encoded in pleasant contexts (Ventura-Bort et al., 2016a,b), and in some studies, no differences were found in memory performance between items encoded in arousing and neutral contexts (Ventura-Bort et al., 2020b, 2019b; Wirkner et al., 2015; Buchwald et al., 2022). These findings indicate that even when high prioritization and long retention intervals are promoted, other factors may need to be considered to clarify the role of emotion in the retrieval of associated neutral information (Madan et al., 2017, 2019, 2020; Ventura-Bort et al., 2020a,b). Some such factors may be related to methodological differences between studies (see also Bogdan et al., 2024), which, in the current case, included variations in the encoding instructions, material used, lab environment, retrieval task employed, or the application of a standardized stress protocol.

One useful approach in investigating this issue is data pooling, which provides an opportunity to comprehensively characterize the effects of emotion on long-term source memory. By increasing overall sample size, the pooling of independent studies with relatively homogeneous experimental designs may favor the exploration of interacting effects and the generalizability of the findings (Boedhoe et al., 2019; Giraudier et al., 2022). Therefore, we conducted a mega-analysis of seven studies ($N = 333$; methodological details of each individual study are summarized in Table 1), to clarify the impact of emotion and potentially interacting factors (i.e., encoding instructions, retrieval task, environmental settings, and stress protocol) on long-term memory performance for emotionally arousing contexts and associated neutral items.

Given that source memory and memory for associated neutral items embedded in emotional contexts may benefit from high prioritization and long-term retention periods (as promoted in the study designs), evidence for a better recollection-based, source contextual memory performance for both pleasant and unpleasant contexts compared to neutral contexts is expected. Similarly, evidence for recollection-driven enhancing effects for items encoded in highly arousing contexts is also hypothesized.

Methods

Participants

We pooled data from previously published and unpublished studies that investigated the effects of emotion on item/context binding in episodic memory. The total sample consisted of 333 healthy young adults ($M_{age} = 23.5$; female = 260, male = 73; Table 1 for gender distribution across samples). All participants provided informed written consent for the experimental protocol, which was approved in accordance with the declaration of Helsinki (Ethic's Approval number: MW 032014_rev_1). A summary of the studies is provided in Table 1.

Stimulus material

In all studies, neutral objects were used as items and pleasant, unpleasant, or neutral pictures as contextual background scenes. Objects were extracted from two different datasets, *The Bank of Standardized Stimuli* (BOSS; Brodeur et al., 2012, 2014) and *the Ecological Adaptation of Snodgrass and Vanderwart* set (Moreno-Martínez and Montoro, 2012). Objects belonged to a variety of different semantic categories (e.g., office supplies, electronics, and household objects) and were grouped in six different sets carefully matched in terms of semantic category, familiarity, object agreement, and manipulability, according to the normative ratings of the standard samples (see BOSS and ecological adaptation of Snodgrass and Vanderwart norms). Background scenes were chosen from the *International Affective Picture System* (IAPS; Lang et al., 2008). Normative valence and arousal ratings were used to categorize the images as pleasant, unpleasant, and neutral. Each contextual background scene was paired with one item.

---

[1] In source memory studies, item memoranda are usually cued, and participants must indicate whether they were previously seen or not during the encoding episode. Source memoranda refer to the recognition of associated information and is typically assessed only when items have been identified as old (e.g., Smith et al., 2004). Additionally, although source and relational memory have been interchangeably used (Eichenbaum et al., 2007) methodological differences between source and relational memory studies have been pointed out (e.g., Chiu et al., 2013). Source memory studies typically examine how, when or where a stimulus was presented (that is the source). These studies use a limited number of alternative choices for each modality (e.g., for when: first or second block; for where: upper or lower part of the screen). On the other hand, relational memory studies assess a more association between items and details of the encoding episode that implies a one-to-one relationship. That is, relational information is trial-unique and as numerous as trials presented (Chiu et al., 2013; Bogdan et al., 2024). Acknowledging these methodological differentiations, here, we refer to source memory when talking about memory for contextual categories and to item memory when describing memory for objects.

TABLE 1 Summary of the study characteristics.

References	Study	Gender W/M	Mean age	Protocol	Groups	Shortened name	*N*	Encoding instruction	Scene categories	Mean valence	Mean arousal	Environment	Retrieval task	Source location	*N* new items	*N* old items/category
Ventura-Bort et al. (2016b)	Study 1	26/3	22.7	–	Control	S1	29	Binding	P/U/N	6.94/2.73/5.27	5.84/5.93/3.51	EEG	O/N	Yes	144	48
Ventura-Bort et al. (2020a)	Study 2	26/4	21.8	–	Control	S2	30	Free viewing	P/U/N	7.02/2.58/5.08	5.88/6.00/3.37	EEG	R/K	Yes	180	60
Ventura-Bort et al. (2019b)	Study 3			Stress	Control	S3-C	30	Binding	P/U/N	7.02/2.58/5.08	5.88/6.00/3.37	EEG	R/K	No	90	60
		58/43	25.57		Stress	S3-S	39	Binding	P/U/N	7.02/2.58/5.08	5.88/6.00/3.37	EEG	R/K	No	90	60
					Stress Delay	S3-SD	18	Binding	P/U/N	7.02/2.58/5.08	5.88/6.00/3.37	EEG	R/K	No	90	60
Wirkner et al. (2015)	Study 4			Stress	Control	S4-C	24	Binding	U/N	2.73/5.27	5.93/3.51	EEG	O/N	Yes	96	48
		56/0	23.48		Stress	S4-S	32	Binding	U/N	2.73/5.27	5.93/3.51	EEG	O/N	Yes	96	48
Ventura-Bort et al. (2020b)	Study 5	26/3	26.68	–	Control	S5	29	Binding	P/U/N	7.14/2.34/5.13	6/6.06/3.25	MRI	R/K	No	132	44
Ventura-Bort et al. (2024)	Study 6	38/37	22.84	Stress	Control	S6-C	32	Binding	P/U/N	7.14/2.34/5.13	6/6.06/3.25	MRI	R/K	No	66	44
					Stress	S6-S	40	Binding	P/U/N	7.14/2.34/5.13	6/6.06/3.25	MRI	R/K	No	66	44
Buchwald et al. (2022)	Study 7	27/3	21.45	–	Control	S7	30	Binding	P/U/N	7.14/2.34/5.13	6/6.06/3.25	Eye tracker	R/K	No	132	44

Column information: Protocol indicates whether a standardized stress protocol was applied; Group indicates whether participants underwent an acute stress induction or not (i.e., control). Groups from studies without stress protocol were also coded as control; Shortened name contains the abbreviation of each study and group. N indicates the number of participants per group; Encoding instruction differentiates between active object/scene binding or passive viewing instructions; Scene categories were either Pleasant (P), Unpleasant (U), or Neutral (N). Mean Valence and Arousal refer to the mean normative score of the scenes used for each category. Environment codes the lab environment in which the experiment took place: EEG lab, eye tracker lab, or MRI scanner. Retrieval task indicates whether a Remember/Know (R/K) or Old/New (O/N) procedure was used. Source location indicates whether participants were instructed to also retrieve the location in which the object was presented during encoding. N New Items and N Old Items/Context codes the number of new items during retrieval and old items per category presented during encoding, respectively.

To ensure that all items were equally paired with the different contextual background categories, item/context category pairings were counterbalanced across participants by creating different lists (for details of list construction see Ventura-Bort et al., 2019a, 2020b), in which items were assigned to different experimental conditions across lists (as old items paired with pleasant, neutral, or unpleasant contexts or as new items; see for details, Ventura-Bort et al., 2020b). Each participant was randomly assigned to one of the lists.

Encoding task

During encoding, items were superimposed on contextual background scenes (Figure 1). The number of item/context pairings encoded varied across studies (see Table 1). Each trial began with the presentation of an item in one of the four quadrants of a black screen. After 3,000 ms, a pleasant, unpleasant, or neutral contextual scene was added as background. The presentation of the item/context pairing lasted 5,000 ms. During that time—in studies 1, 3–7—participants were instructed to imagine the object as a part of the scene—to facilitate item-context binding—and to indicate whether the imagination was successful or not by pressing a button after item/context offset (e.g., Ventura-Bort et al., 2016a,b). In study 2, the item/context pairings were presented in a free viewing condition without an active binding instruction (Ventura-Bort et al., 2019a, 2020a). In all studies, a fixation cross was presented continuously during all item/context trials, to which participants were instructed to look at during the task. Participants were never informed about the subsequent retrieval task (i.e., incidental encoding).

Retrieval task

Approximately 1 week after encoding, participants came back to the lab to perform the retrieval task in which previously encoded items were presented intermixed with new ones in a pseudo-randomized fashion (Figure 1). The number of new items varied across studies (see Table 1). In each recognition trial, an item was presented in the center of the screen without context for 3,000 ms. After item offset, a question was shown to which participants were instructed to indicate whether the item was seen during encoding. In studies 2, 3, 5–7, the Remember/Know procedure was implemented (Tulving, 1985) and the “Remember/Know/New?” question was asked here. For that, participants were instructed to press the “Remember” button when they recognized the item as shown during encoding and could bring back specific associated information that occurred during encoding (e.g., thoughts evoked by the object when seen for the first time). The “Know” button was required when the item was recognized as presented during encoding but without retrieval of specific associated information, and participants were instructed to press the “New” button when the item was not seen during encoding.[2] In studies 1 and 4, participants were presented with the “Old/New?” question and instructed to press the “Old” button if they recognized the item as old or else the “New” button.

If participants made “Old” judgments (“Remember” or “Know” judgments in studies 2, 3, 5–7), follow-up questions about source information were presented. In all studies, participants were instructed to indicate the category (e.g., pleasant, unpleasant, and neutral) of the contextual background scene that was paired with the item during encoding. In studies 1, 2, and 4, prior to the context-related question, participants were asked to retrieve the location the item was presented at during encoding (i.e., which quadrant of the screen). In all studies, tasks were programmed with Presentation (Neurobehavioral Systems Inc., Albany, CA, USA).

Lab environment

The included studies took place in three different lab environments. Studies 1–4 were carried out in an EEG lab. These experiments took place in a sound-attenuated, dimly lit room and participants were seated in a comfortable chair (e.g., Ventura-Bort et al., 2016a,b). Participants in studies 5 and 6 performed both the encoding and retrieval session in the MRI scanner (Ventura-Bort et al., 2016a,b). Study 7 took place in an eye-tracking lab. Here, the participants’ head was positioned in an eye tracker and eye movements were continuously recorded during encoding and retrieval.

Stress protocol

In studies 3, 4, and 6, participants underwent a stress protocol prior to the encoding session. In each of the three studies, participants were randomly assigned to either a stress or control condition. In the stress condition, participants were exposed to the Socially Evaluated Cold Pressure Test (SECPT; for stress and control protocol, see Schwabe et al., 2008; Schwabe and Schächinger, 2018) followed by a difficult mental arithmetic test (see for similar test, Smeets et al., 2012). The stress induction lasted 15 min. After, participants were informed about the two-part protocol by a cold and unsociable experimenter, in the first part, they were asked to immerse their right hand down to the wrist into ice water (temperature: 0–3°C) for 3 min (or until they could no longer tolerate it). During hand immersion, participants were instructed to look straight into a camera because their faces were videotaped. They were told that video recordings would later be analyzed for facial expressions. Thereafter participants performed the second part of the stress condition protocol consisting of a

---

[2] As part of the instructions, participants were also given the following example: Imagine that you are in the supermarket, and in front of you there is a person with a red t-shirt that is talking to her partner about their holidays. Few days later, you see the same person on the street. If you can then recognize the person and retrieve any contextual information about the first encounter (where you saw her for the first time, what she was wearing, what she was talking about, what you thought when you saw her), that is an example of “remembering” her. However, if you can recognize her, but are not able to identify from where, or retrieve any specifics, then is an example of “knowing” her.

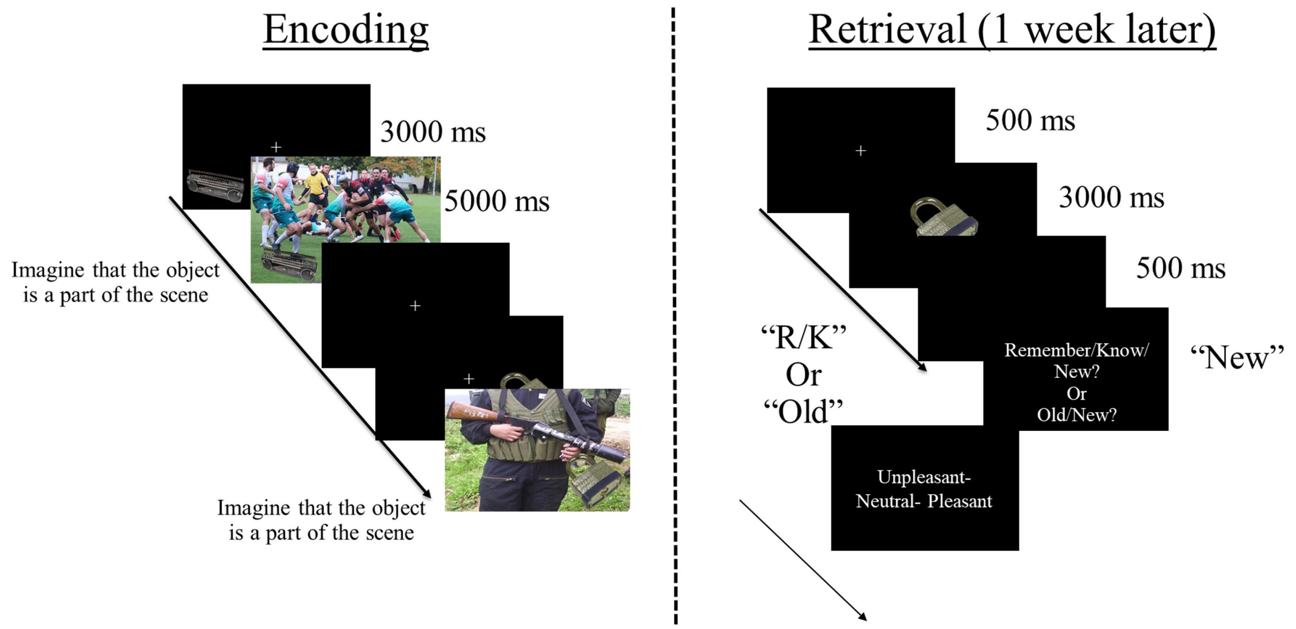


FIGURE 1
Schematic representation of the task design. During encoding, participants incidentally viewed different, everyday objects (office supplies, electronics, and household objects) presented in one of the four quadrants of the screen, overlaid on different background scenes that were either pleasant, neutral or unpleasant. In most studies (1, 3–7; except study 2) participants were also instructed to imagine that the object is a part of the scene during viewing the object/scene combination. During retrieval, participants viewed the encoded objects intermixed with new objects and performed a recognition task, using either a Remember/Know paradigm or an Old/New paradigm. If objects were recognized as old [i.e., Remember (R), Know (K), or Old judgments], participants were asked to retrieve the associated scene background (pleasant, unpleasant, or neutral).

difficult 5-min mental arithmetic test in which they had to count backwards as fast and accurately as possible in steps of 17 starting at 2043. Whenever they counted too slowly or mistakenly, they received negative feedback (i.e., to count faster or start over again at 2043).

In the control condition, participants were received by a friendly and socially interacting experimenter. Firstly, participants immersed their right hand down to the wrist for 3 min in warm water (35–37°C). They were not videotaped. Secondly, they performed a simple arithmetic task in which they had to count consecutively from 1 to 25 at their own pace and had to start anew at 1 when having reached 25. In all three studies, participants in the control and stress condition performed the encoding session ~30 min after the stress induction (control) protocol. A subgroup in study 2 (stress delay), performed the encoding session 180 min after the stress induction.

Behavioral data recording and analysis

Behavioral performance for items and source contextual information was recorded using Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) and analyzed using RStudio. Data preprocessing was conducted using *tidyverse* (Wickham et al., 2019). Memory performance for items (i.e., objects) and source contextual details (i.e., emotional category of background scenes) was examined in two different sets of analysis. D prime [d'; z(P Old) – z(P False Alarm)] was used as an index for item memory. For source contextual memory, which was assessed based on participants' responses to the emotional category of the contextual background scene that was paired with the object during encoding, the unbiased hit rate (Hu) was calculated (Ventura-Bort et al., 2020a; Wagner, 1993). The *Hu* index takes into account not only the stimulus performance but also the judge performance and is defined as the conjoint probability of the correct identification of a stimulus and the correct use of a response (Wagner, 1993; see for details Ventura-Bort et al., 2020b).

In the first set of analyses, memory performance was coded independently of memory type. Therefore, Remember and Know judgments that were obtained in studies using the Remember/Know procedure, were indistinctively coded as "Old" judgments.

In the second set of analyses, a distinction between Remember and Know judgments was made. It is important to note that analysis of familiarity and recollection processes in explicit memory retrieval is constrained by the assumption that both processes are interrelated. However, this relation can be exclusive or independent (Yonelinas and Jacoby, 1995). Theoretical proposals and empirical data clearly support the independence assumption as a more appropriate index to differentiate between recollection and familiarity processes (Yonelinas and Jacoby, 1995; Yonelinas, 2002). Thus, we decided to control for dependency (see for details Ventura-Bort et al., 2020a). d' was therefore calculated under the independence assumption for both Remember (d' Recollection = z(P Remember) – z(P False Alarm Remember)) and Familiarity:

$$z\left(\frac{P\ Know\ Hit\ Rate}{1 - P\ Remember\ Hit\ Rate}\right) - z\left(\frac{P\ Know\ False\ Alarm}{1 - P\ Remember\ False\ Alarm}\right)$$

For source memory, the interaction effects of context and memory processes were analyzed by calculating the Hu indexes for each affective category and memory judgment, separately. Specifically, the Hu indexes for Remember and Know judgments, were calculated by only taking into consideration items that were judged as remembered or known, respectively. For instance, for neutral contexts of objects restricted to Know judgments, the Hu was calculated as follows:

$$\frac{\textit{Hit Know Neutral Context}}{(\textit{Hit Know Neutral Context} + \textit{Incorrect Know Neutral Context})} * \frac{\textit{Hit Know Neutral Context}}{N^{\circ}\ \textit{of times Neutral Context is chosen under Know judgements}}$$

Hit Know Neutral Context = Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was correctly identified*; Incorrect Know Neutral Context* = Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was not correctly identified; *N° of times Neutral Context is chosen under Know judgments* = Number of objects whose background was labeled as "Neutral," including those whose background was wrongly identified.

For each participant, memory performance was averaged across affective category (e.g., pleasant, neutral, and unpleasant) and, when required, split by memory type (i.e., Remember, Know).

The effects of affective category on memory for items (as indexed by d') and source contextual details (as measured by Hu) were tested with linear mixed models (LMM) using *lme4* (Bates et al., 2012). In the first set of analysis, as fixed effects, we specified *Affective category* (e.g., pleasant, neutral, and unpleasant), *Encoding instructions* (i.e., binding, free viewing), *Group* (i.e., control, stress, and stress delay), *Retrieval task* (Old/New, Remember/Know procedure), *N new items* (i.e., number of new items presented during retrieval), and *Environment* (i.e., EEG, MRI, and Eye tracker) and their associated interactions. In the second set of analyses, the fixed factor *Memory type* (i.e., Remember, Know) was further added. *Participant* as well as a new dummy variable called *Study group* consisting of a combination of *Group* (i.e., control, stress, and stress delay) and *Study* (i.e., studies 1–7) were modeled as random effects.

Because the main focus of this mega-analysis was to clarify the role of potential factors modulating memory performance, particularly in interaction with *Affective category*, the effects of methodology-related factors were included in the analyses (i.e., *Encoding instructions*, *Retrieval task*, *N new items*, *Environment*, and *Group*) using a parsimonious model selection [following the general recommendations by Bates et al. (2012) and without knowledge or consideration of fixed-effect estimates]. Notably, the parsimonious model selection always considered the fixed-effect estimates of *Affective category*. For model comparisons, the χ^2-distributed likelihood ratio and its associated p-value was used. All analyses were conducted using full information maximum likelihood modeling. If significant effects were found (or exploratory analysis conducted), they were followed up by *post-hoc* comparisons using *lsmeans* (Lenth, 2016), correcting for multiple comparisons (Tukey's honest significant difference; HSD; Tukey, 1949).

Although the significant effects ($p < 0.05$) that could arise from the mixed model analyses may inform about the probability, under the assumption of no difference between conditions (H_0; i.e., no effects of affective category on memory performance are observed), of obtaining a result equal to or more extreme that what was actually found, they do not inform about the extent of acceptance/rejection of the alternative hypothesis (H_1; i.e., positive effects of affective category on memory performance) *per se* (Greenland et al., 2016; Held and Ott, 2018). To address this issue, we additionally used Bayes analysis (Wagenmakers et al., 2018) to evaluate our hypotheses. Using a Bayesian approach for hypothesis testing encompasses the calculation of the predictive adequacy of two competing models, to quantify the evidence provided by the data for one model over the other (Wagenmakers et al., 2018). To test the evidence in favor of the alternative hypotheses, we calculated the Bayes factor (BF_{10}) on the significant effects by comparing final models to null models (i.e., models without the significant effects of interest). For instance, to test the effects of *Affective category* on item memory, the model including such a factor will be tested against an identical model without the *Affective category* factor. To interpret the results of the Bayes factors, the following classification was used (Lee and Wagenmakers, 2013): a BF_{10} larger than 100 provides decisive evidence in favor of H_1, a value between 30 and 100, indicates very strong evidence for H_1, a score between 10 and 30 provides moderate evidence for H_1, a value between 1 and 3 indicates anecdotal evidence for H_1, a BF_{10} of 1 provides no evidence for either H_1 or H_0. On the other hand, values between 0.3 and 1 provide anecdotal evidence for H_0, values between 0.1 and 0.3 indicate moderate evidence for the H_0, scores between 0.03 and 0.1 show strong evidence for H_0, values between 0.01 and 0.03 indicate very strong evidence for H_0, and values lower than 0.01 provide decisive evidence for H_0.

Results

Tables 2–5 contain the results of the linear mixed models for all analyses.

Memory for items

Effects of affective category independently of memory type

The most parsimonious model that described the data best included—in addition to *Affective category*—the factors *Encoding instructions, Retrieval task,* and *Environment* as fixed factors (Table 2). Interactions between fixed factors did not improve the model and were thus not included.

Results showed an effect of *Affective Category,* with higher memory performance for items from pleasant (but not from unpleasant) compared with neutral contextual background scenes (Figure 2A). Follow-up analysis revealed higher memory performance for objects encoded in pleasant, compared to both neutral, $t_{(610)} = 3.18$, $p = 0.004$, and unpleasant contexts, $t_{(610)} = 2.66$, $p = 0.02$, but no memory differences were found between objects from unpleasant and neutral backgrounds, $t_{(608)} = 0.55$,

TABLE 2 Linear mixed model predicting memory performance for items independently of memory type (*N* participants = 333; *N* observations = 943).

Predictors	D prime				
	b	*SD*	*CI*	*t*	*p*
(Intercept)	0.54	0.09	0.37 – 0.72	6.04	**<0.001**
Affective category					
Pleasant	**0.06**	**0.02**	**0.02 – 0.09**	**3.18**	**0.002**
Unpleasant	0.01	0.02	−0.02 – 0.04	0.55	0.582
Encoding instructions					
Binding	**0.62**	**0.10**	**0.42 – 0.82**	**5.98**	**<0.001**
Retrieval task					
Old/new	**0.90**	**0.07**	**0.75 – 1.04**	**12.17**	**<0.001**
Lab					
MRI	**0.31**	**0.07**	**0.17 – 0.45**	**4.37**	**<0.001**
Eye tracker	0.13	0.10	−0.07 – 0.33	1.32	0.189

Bold values indicate significant effects, $p < .005$.

$p = 0.84$. However, the Bayes factor indicated strong evidence in favor of a model without the *Affective Category* factor ($BF_{10} = 0.24$; see Table 6).

A significant effect of *Encoding instructions* revealed better memory performance when participants were instructed to bind objects and background scenes, compared to when they were asked to attentively view the item/context pairings (Figure 2B). An effect of *Retrieval task* was also found, indicating that memory performance was better when the Old/New task was used, in comparison to the Remember/Know procedure (Figure 2C). Finally, a significant effect of *Environment* revealed higher memory performance in the MRI scanner (but not in the Eye tracker environment), compared to the EEG lab (Figure 2D). *Post-hoc* comparison confirmed differences between the EEG and MRI environment, $t_{(5.04)} = 4.29$, $p = 0.017$, but no differences were observed between either the EEG and eye tracker, $t_{(5.87)} = -1.31$, $p = 0.44$, or MRI and eye tracker environments, $t_{(5.65)} = 1.73$, $p = 0.27$. The effects of *Encoding instructions, Retrieval task,* and *Environment* were supported by decisive evidence in favor of inclusion of these factors in the model (BF_{10}s > 100).

Effects of affective category as a function of memory type

The simplest, best fitting model included—in addition to *Affective category*– the factors *Memory type, Encoding instructions,* and *Environment* as fixed factors. Including interactions between *Memory type* and *Affective category* improved the model significantly. No other fixed factors or interactions between fixed factors explained the data better and were thus not included (Table 3).

A *Memory type* effect revealed higher memory performance under Know than Remember judgments. As in our previous model, significant effects of *Encoding Instructions* and *Environment* were found (see also Table 6 for Bayes factors). Interestingly, in the absence of a significant main effect of *Affective Category,* a significant interaction effect between *Memory type* **Affective category* was found, indicating higher memory performance for objects embedded in pleasant backgrounds compared with neutral ones, particularly when memory was based on recollection (Remember judgments; Figure 3). These results were confirmed in follow-up analyses, indicating no differences between affective categories in Know judgments [pleasant vs. neutral: $t_{(1,229)} = 0.54$, $p = 0.85$; pleasant vs. unpleasant: $t_{(1,229)} = 0.52$, $p = 0.86$; unpleasant vs. neutral: $t_{(1,229)} = 0.01$, $p = 0.99$], but higher memory performance for objects from pleasant contexts for Remember judgments [pleasant vs. neutral: $t_{(1,229)} = 4.13$, $p < 0.001$; pleasant vs. unpleasant: $t_{(1,229)} = 2.33$, $p = 0.05$]. However, no differences were found between objects from unpleasant and neutral contexts: $t_{(1,229)} = 1.80$, $p = 0.17$. Despite the significant interacting effects, the Bayes Factor indicated moderate evidence in favor of a model without the interaction *Memory type* * *Affective Category* ($BF_{10} = 0.1$).

Memory for source contextual details

Effects of affective category independently of memory type

The simplest, best fitting model included –in addition to *Affective category*– the fixed factors *Encoding instruction,* and *Retrieval task.* Because interaction effects did not improve the model, they were not included. Results revealed a significant effect of *Affective category,* indicating higher memory performance for neutral, compared to pleasant and unpleasant contexts (Table 4, Figure 4A). However, no differences between pleasant and unpleasant contexts were observed, $t_{(608)} = -0.79$, $p = 0.71$. Moreover, *Retrieval task* effects revealed higher source memory performance when participants executed the Old/New task, in comparison with the Remember/Know procedure (Figure 4B). The Bayes factor indicated decisive evidence in favor of the inclusion of the three factors in the model (BF_{10}s > 100).

TABLE 3 Linear mixed model predicting item memory performance as a function of memory type (*N* participants = 247; *N* observations = 1,481).

Predictors	D prime				
	b	*SD*	*CI*	*t*	*p*
(Intercept)	**1.02**	**0.05**	**0.92 – 1.13**	**18.67**	**<0.001**
Memory type					
Remember	**−0.21**	**0.05**	**−0.30 to −0.12**	**−4.63**	**<0.001**
Affective category					
Pleasant	0.02	0.05	−0.06 – 0.11	0.54	0.592
Unpleasant	0.00	0.05	−0.09 – 0.09	0.01	0.993
Encoding instructions					
Binding	**0.48**	**0.09**	**−0.66 to −0.30**	**−5.19**	**<0.001**
Lab					
MRI	**0.26**	**0.06**	**0.14 – 0.38**	**4.12**	**<0.001**
Eye tracker	**0.18**	**0.09**	**0.00 – 0.36**	**1.98**	**0.049**
Remember * Pleasant	**0.16**	**0.06**	**0.04 – 0.29**	**2.54**	**0.011**
Remember * Unpleasant	0.08	0.06	−0.04 – 0.21	1.27	0.205

Bold values indicate significant effects, $p < .005$.

TABLE 4 Linear mixed models predicting source memory performance independently of memory type (*N* participants = 333; *N* observations = 940).

Predictors	Hu				
	b	*SD*	*CI*	*t*	*p*
(Intercept)	0.11	0.07	−0.02 – 0.24	1.69	0.091
Affective category					
Pleasant	**−0.05**	**0.01**	**−0.06 to −0.03**	**−7.24**	**<0.001**
Unpleasant	**−0.04**	**0.01**	**−0.05 to −0.03**	**−6.91**	**<0.001**
Encoding instructions					
Binding	0.05	0.07	−0.09 – 0.18	0.66	0.506
Retrieval task					
Old/new	**0.19**	**0.05**	**0.10 – 0.28**	**4.17**	**<0.001**

Bold values indicate significant effects, $p < .005$.

Effects of affective category as a function of memory type

When memory was split into Remember and Know judgments, the best fitting model included –in addition to *Affective category*– the fixed factors *Memory type, Environment,* and *Encoding instructions.* The interactions between *Memory type* and *Affective category,* between *Memory type* and *Environment*, and between *Memory type, Affective category,* and *Group* were also included, given that they improved the model fit (Table 5). A significant main effect of *Affective category* revealed overall higher memory performance for neutral contexts. A main effect of *Encoding instructions* was also observed, with better source memory performance when object/scene pairings were actively bound during encoding. The Bayes factors indicated decisive evidence in favor of the inclusion of these factors in the model (BF$_{10}$s > 100; see Table 6). A significant interaction between *Memory type* * *Affective category* revealed higher memory performance for both pleasant and unpleasant contexts when memory was mediated by recollection (Remember judgments; BF$_{10}$ > 100). Follow-up analyses confirmed higher memory performance for objects receiving Remember, compared to Know judgments, for pleasant, $t_{(1,216)} = 8.13$, $p < 0.001$, and unpleasant contexts, $t_{(1,215)} = 6.07$, $p < 0.001$, but not for neutral ones, $t_{(1,215)} = 0.31$, $p = 0.75$. *Environment* also interacted with *Memory type,* showing higher source memory performance related to Remember judgments in the MRI scanner and Eye tracker lab compared to the EEG environment (BF$_{10}$s > 100). *Post-hoc* comparisons showed higher contextual memory under Remember than Know judgments in the three environments, *ts* > 3.71, *ps* < 0.001, but recollection-based memory was higher in the MRI, compared to the EEG environment, $t_{(4.05)} = 5.91$, $p = 0.009$. No other differences were observed (|*ts*| < 2.15, *ps* > 0.205).

Finally, a three-way interaction between *Memory type* Affective Category* Group* revealed source memory performance for pleasant and unpleasant contexts based on Remember judgments, especially for participants in the stress group (Figure 5). Following-up on the

TABLE 5 Linear mixed model predicting source memory performance for source details as a function of memory type (*N* participants = 247; *N* observations = 1,479).

Predictors	Hu				
	b	*SD*	*CI*	*t*	*p*
(Intercept)	**0.14**	**0.02**	**0.11 – 0.18**	**8.54**	**<0.001**
Memory type					
Remember	−0.03	0.02	−0.07 – 0.01	−1.56	0.12
Affective category					
Pleasant	**−0.05**	**0.02**	**−0.09** to **−0.02**	**−3.07**	**0.002**
Unpleasant	**−0.04**	**0.02**	**−0.07** to **−0.01**	**−2.26**	**0.024**
Lab					
MRI	0.01	0.01	−0.02 – 0.04	0.77	0.444
Eye tracker	−0.02	0.02	−0.06 – 0.03	−0.82	0.411
Encoding instructions					
Passively watching	**−0.04**	**0.02**	**−0.08 – 0.06**	**−2.11**	**0.035**
*Memory type * Affective category*					
Remember*Pleasant	**0.14**	**0.02**	**0.09 – 0.19**	**5.84**	**<0.001**
Remember*Unpleasant	**0.08**	**0.02**	**0.03 – 0.12**	**3.12**	**0.002**
*Memory type * Lab*					
Remember*MRI	**0.08**	**0.02**	**0.04 – 0.11**	**4.52**	**<0.001**
Remember*Eye tracker	**0.07**	**0.03**	**0.01 – 0.12**	**2.53**	**0.012**
*Memory type*Affective Category* Group*					
Know*Neutral*Stress	0.01	0.02	−0.04 – 0.05	0.30	0.763
Remember*Neutral*Stress	−0.01	0.02	−0.05 – 0.04	−0.26	0.793
Know*Pleasant*Stress	0.01	0.02	−0.05 – 0.03	−0.45	0.652
Remember*Pleasant*Stress	**0.05**	**0.02**	**0.01 – 0.10**	**2.20**	**0.028**
Know*Unpleasant*Stress	−0.02	0.02	−0.07 – 0.02	−1.00	0.318
Remember*Unpleasant*Stress	**0.09**	**0.02**	**0.04 – 0.13**	**3.87**	**<0.001**
Know*Neutral*Stress Delay	0.02	0.04	−0.05 – 0.05	−0.81	0.418
Remember*Neutral*Stress Delay	−0.03	0.04	−0.11 – 0.05	−0.81	0.418
Know*Pleasant*Stress Delay	0.04	0.04	−0.04 – 0.12	0.89	0.376
Remember*Pleasant*Stress Delay	−0.00	0.04	−0.08 – 0.08	−0.01	0.995
Know*Pleasant*Stress Delay	0.03	0.04	−0.05 – 0.11	0.03	0.486
Remember*Pleasant*Stress delay	0.01	0.04	−0.07 – 0.09	0.34	0.736

Bold values indicate significant effects, $p < .005$.

interacting effects, we carried out *post-hoc* comparisons between groups on source memory for each memory type and affective category, separately. For familiarity-based contextual memory, no differences between groups on any of the affective categories were observed ($ps > 0.99$; Figure 5A). However, for recollection-based memory, a trend emerged, indicating that participants in the stress, compared to the control, showed higher memory performance for unpleasant contexts: $t_{(21.5)} = 3.86$, $p = 0.057$ (Figure 5B). No further significant differences were found ($|ts| < 2.20$, $ps > 0.73$). Bayes factor provided moderate evidence in favor of a model without the triple interaction effect ($BF_{10} = 0.29$).

Discussion

The primary goal of the current study was to further our understanding of the effects of emotion on memory for source contextual details and associated neutral items. Capitalizing on a large sample size ($N = 333$) derived from pooling together data from seven different studies with similar experimental designs, we investigated the modulatory effects of emotion as well as potential interacting factors (e.g., encoding instructions, type of retrieval task, lab environment, or the application of a stress protocol) on memory binding for associated items (objects) and source

TABLE 6 Summary of the main findings of the Bayes factor to test for the significant effects observed in the best fitting models for item memory and source contextual memory.

	Model description	Formula	Bayes factor output (BF_{10})							
			Affective category	Encoding instruction	Retrieval task	Lab	Memory type	Affective category * Memory type	Memory type * Lab	Affective category*Memory type* Group
Memory for items	Effects of affective category independently of memory type	*D' ∼ Affective category + Encoding instructions + Retrieval task + Lab*	0.024	>100	>100	>100	—	—	—	—
	Effects of affective category and Memory type	*D' ∼ Affective category * Memory type+ Encoding instructions + Lab*	0.027	>100	—	>100	14.61	0.11	—	—
Memory for contexts	Effects of affective category independently of memory type	*Hu∼ Affective category + Encoding instructions + Retrieval task*	>100	>100	>100	—	—	—	—	—
	Effects of affective category and Memory type	*Hu∼ Affective category * Memory type + Memory type * Environment + Encoding instructions + Affective category: Memory type: Group*	>100	62.27	—	>100	>100	>100	>100	0.29

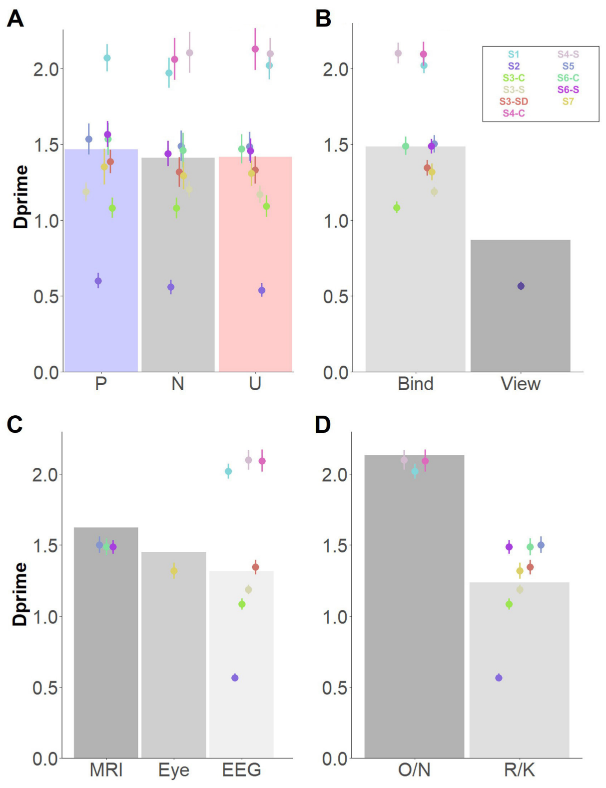


FIGURE 2
Main significant effects for memory for items, independently of memory type. Dots depict averaged values across study and group. Error bars represent standard errors. Bar plots depict the estimated means from the linear mixed model. **(A)** Main effect of affective category; **(B)** Main effect of encoding instructions; **(C)** Main effect of retrieval task; **(D)** Main effect of Environment. O/N, Old/New task; R/K, Remember/Know procedure.

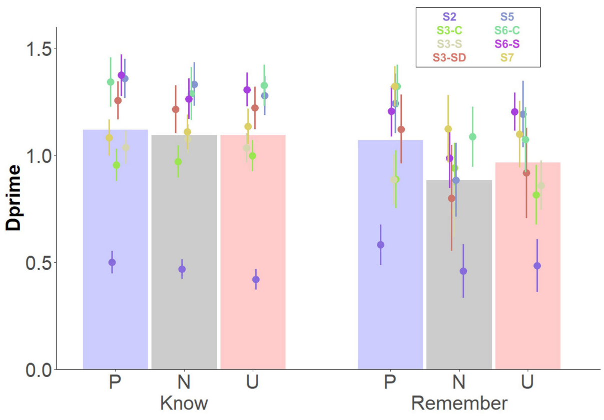


FIGURE 3
Interacting *Affective category* and *Memory type* effects on memory performance for items. Dots depict averaged values across study and group. Error bars represent standard errors. Bars depict the estimated means from the linear mixed model for the interaction *Affective category * Memory type*.

contextual details (emotional category of background scenes). Linear mixed models revealed a recollection-based retrieval advantage (i.e., uniquely for Remember judgments) for unpleasant

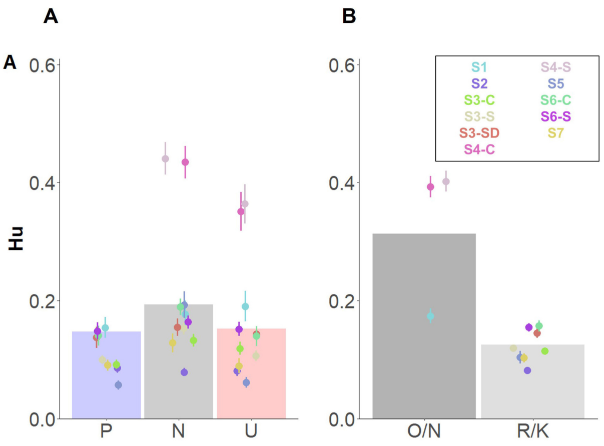


FIGURE 4
Main effects of source memory independently of memory type. Dots depict averaged values across study and group. Error bars represent standard errors. Bar plots depict the estimated means from the linear mixed model. **(A)** Main effect of *Affective category*; **(B)** Main effect of *Retrieval task*. O/N, Old/New task; R/K, Remember/Know procedure.

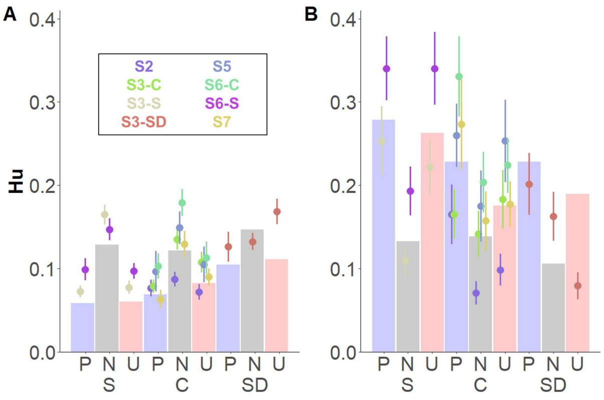


FIGURE 5
Interacting effects of *Affective category*, *Memory type*, and *Group* for memory for source details. Dots depict averaged values across study and group. Error bars represent standard errors. Bar plots depict the estimated means from the linear mixed model. **(A)** Depicts know judgments and **(B)** remember judgments both split by group: stress (S; left), control (C; middle), and stress delay (SD; right).

and pleasant source contextual details compared with neutral ones. Bayes hypothesis-testing analysis further indicated decisive evidence in favor of the interacting affective category (pleasant vs. unpleasant vs. neutral) and memory type (recollection vs. familiarity) effects, providing support for a relevant role of these factors in source contextual memory. Regarding item memory, linear mixed models uncovered enhanced memory for items encoded in pleasant contexts compared with their neutral and unpleasant counterparts, particularly for Remember judgments. However, Bayes analysis revealed strong to moderate evidence for models without *Affective Category* (or its interactions), indicating that the affective context in which objects were placed during encoding had little influence on item memory performance. Furthermore, we observed decisive evidence for modulating effects of encoding instructions, retrieval task, and lab environment. Below, we will discuss these results with regards to available evidence and the current neurobiological models of emotional episodic memory and also add *predictive processing* as a theoretical framework that may be useful in understanding the effects of emotion on memory for source details and associated neutral information.

Based on the existing neurobiological models of emotional episodic memory (e.g., McGaugh, 2004; Mather et al., 2016), the current studies (all part of the mega analysis) were designed to promote the positive effects of emotion on source memory, by facilitating item-context integration (i.e., high prioritization of items) and fostering consolidation processes. Under these circumstances, a recollection-based memory advantage for highly arousing (both pleasant and unpleasant) source contextual details was observed in our pooled data analysis. Contrary to our hypothesis, however, no evidence was found for effects of emotion on memory for associated neutral information (i.e., item memory). Neuroimaging studies have shown that the hippocampus, as well as connected cortical regions within the posterior parietal cortex (King et al., 2015; Ranganath and Ritchey, 2012; Rugg and Vilberg, 2013) may play an important role in recollection-based processes (Eichenbaum et al., 2007; Yonelinas et al., 2002), especially for highly arousing material (Maddock et al., 2001, 2003). Interpreted within the above-mentioned models (Mather et al., 2016; McGaugh, 2004), high prioritization and long retention period may have facilitated the initial encoding of emotionally relevant information (Kensinger, 2009; Salsano et al., 2024), by engaging limbic and para-limbic regions (e.g., Pedale et al., 2019) and the subsequent NA and corticosteroids action in memory sensitive regions, such as the hippocampus, favoring both encoding and consolidation of affectively-laden contextual details that led to better recollection-based retrieval.

Although no evidence in favor of additional interacting effects of affective category with other experimental manipulations was found, memory performance was modulated by encoding instructions, retrieval task, and environmental settings in isolation. Participants' memory performance was better when they were instructed to actively bind objects and background scenes relative to when they just attended to pairs of stimuli, individually. During the "binding" instructions, participants were asked to effortfully combine item/context pairings which likely triggered deeper encoding than during the relatively effortless "just viewing" instructions. These findings are in line with earlier studies showing that the depth of processing enhances subsequent memory retrieval (Craik and Tulving, 1975; Hanslmayr et al., 2009).

In addition to the instructions given during encoding, the task used during retrieval also modulated memory performance. Specifically, memory for items and contexts was better when using the simpler Old/New task compared to the Remember/Know procedure. Previous studies testing the effects of retrieval tasks on memory performance have consistently found differences between these two paradigms (Eldridge et al., 2002; Gardiner et al., 1998; Hicks and Marsh, 1999). The usage of a single Remember/Know procedure compared with a two-step procedure (i.e., the Old/New question followed by the Remember/Know question), has been associated with a more liberal response bias (Hicks and Marsh, 1999) and more false alarms, particularly for "Know" judgments (Eldridge et al., 2002), suggesting that memory judgments are susceptible to differences in task instructions. Our findings replicate these observations showing decreased discriminability of item and source information under the Remember/Know procedure.

We also found that memory performance was modulated by the environment in which the task was conducted. Memory for items was enhanced in the MRI compared to the EEG environment. In the same vein, higher recollection-based memory for contextual scenes was found in the MRI setting. One of the unique characteristics of the MRI environment in relation to other experimental settings is the loud scanner noise that is constantly delivered during the task. This noise, which is often perceived as annoying, aversive or stressful could influence cognitive processes while participants perform tasks in the scanner. Previous studies have shown that the scanner environment not only increases cortisol levels (Tessner et al., 2006) but such a moderately stressful event might also favor task engagement, leading to performance improvements (Plessow et al., 2011). To systematically test whether the influence of MRI noise on cognitive performance, Hommel et al. (2012) investigated whether task performance in an MRI environment was modulated by the presence vs. absence of MRI noise. The authors observed that scanner noise favors cognitive control by reducing the influence of potential distractors (Hommel et al., 2012). Our results may thus indicate that the MRI environment helped participants stay focused on the encoding and retrieval tasks, resulting in better memory performance, particularly compared to the EEG environment.

Altogether, our findings emerging from the mega-analysis of prior individual studies suggest that highly arousing contexts facilitate the encoding and subsequent retrieval of source contextual details. Existing neurobiological models of emotional memory postulate that under high prioritization and long retention intervals that promote consolidation processes (Mather et al., 2016), and as such, the memory enhancing effects of emotional events may extend to associated neutral information. However, inconsistent with the prior interpretation, for item memory we found strong evidence in favor of models without the *Affective Category* factor (or interactions), suggesting that alternative perspectives may also have to be considered to understand the relationship between emotion and memory source details and associated neutral information (see also Bogdan et al., 2024, for evidence regarding the impact of emotion on item-context binding when the emotional information is manipulated in the items' content).

An alternative view explaining our emotional source memory findings could be the *Predictive Processing account* (e.g., Clark, 2013; Friston et al., 2017; Hutchinson and Barrett, 2019; Hohwy, 2013), which posits that the brain is an active entity that is continuously making predictions about the future (e.g., Bastos et al., 2012; Friston, 2010; Rao and Ballard, 1999; Sterling and Laughlin, 2015). Relevant for the present study, predictive processing has been integrated into recent accounts of affective processing as well as its impact on learning and memory, and the associated neural mechanisms (Cross et al., 2018; Ferreira-Santos, 2016; Kalbe and Schwabe, 2020, 2022; Meaux et al., 2019; Rouhani et al., 2023; Strube et al., 2021).

Critically, the predictive processing framework can be used to further understand the current inconsistent memory findings for item and source contextual details. Because the brain is constantly generating predictions about incoming sensory inputs based on past experience and encoding prediction errors, brain activity and ensuing mental experience in a given trial occur as a function of what one has experienced in previous trials, suggesting that brain activity and affective experience observed over the course of an experiment are temporally dependent. Furthermore, predictions about sensory stimuli can develop over a longer timescale (e.g., across the lifespan), which inevitably vary from one subject to another and may be hard to modify through exposure to stimuli in a laboratory setting (Lee et al., 2021). One possibility, therefore, is that the processing and subsequent retrieval of contextual scenes is influenced by previously encountered events that determine the probability of their occurrence to a greater extent than that of isolated items (e.g., Strube et al., 2021). The recollection-based advantage for emotionally arousing source contextual details observed in the present data pooling study could thus be partly the consequence of their unpredictability (i.e., prediction error) in comparison to neutral contexts (Schwartz, 1997; Schwartz et al., 2002). On the other hand, the formation of item-context associations may be simultaneously influenced by different factors that have opposing effects on memory. Although emotional (unpredictable) contexts may favor the storage of the encountered information, the resources devoted to process the details of the composition (i.e., precision signals) could both enhance the memory of the associated items, if such resources are dedicated to item processing, or diminish it if invested in the processing of other details. The interplay of these opposing effects could have, thus, also led to the lack of evidence of emotional effects on item memory. Future studies may therefore also use a predictive processing framework to interpret the effects of emotion on memory for source details and associated neutral information and also considering sources of variability (e.g., chain of previously seen events, personal experiences with similar contexts; c.f., recent work on source memory: e.g., Ben-Yakov et al., 2022; Greve et al., 2017; Kafkas and Montaldi, 2018; Kalbe and Schwabe, 2020, 2022; Ortiz-Tudela et al., 2021; Quent et al., 2022; Van Kesteren et al., 2012).

In contrast to individual studies, the mega-analysis approach used here benefits from a larger sample size to draw more solid conclusions. However, it should be noted that the samples of the current studies were relatively homogeneous and included young healthy adults, mostly women. The homogeneity of the collapsed samples may pose constraints for the generalization of the results to older and more gender-balanced populations. This is particularly important considering that previous studies have reported gender (Canli et al., 2002; De Goede and Postma, 2008; Guillem and Mograss, 2005) and age differences in memory retrieval (Rhodes et al., 2019). Future studies investigating the impact of these demographic characteristics on emotional source memory would lead to further insights in this field. Additionally, future studies should also consider combining mega-analysis with other machine learning-based validation approaches like cross-validation leave-one-out approaches that could further inform about the reliability and generalizability of the results across samples.

Conclusions

In the current study, we aimed at extending our understanding of the effects of emotion on item/context memory binding. Pooling data from seven different studies ($N = 333$), we observed a recollection-based emotional enhanced source contextual memory, in line with existing neurobiological models of emotional episodic memory (Mather et al., 2016; McGaugh, 2004). However, for item memory Bayes hypothesis-testing revealed strong evidence in favor of models without the *Affective Category* factor. The current findings also invites to consider alternative perspectives, such as the predictive processing, to better understand the relationship between affective relevance and source memory. Future work might benefit from considering sources of variability (e.g., chain of previously seen events, personal experiences with similar contexts) that are otherwise labeled as random error in clarifying when and why affective relevant information might show differential effects on source memory.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://osf.io/bxdvg/.

Ethics statement

The studies involving humans were approved by Ethic Committee of University of Greifswald. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

CV-B: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. YK: Writing – original draft, Writing – review & editing. JWi: Data curation, Investigation, Writing – original draft. JWe: Writing – review & editing. LS: Writing – review & editing. AH: Writing – review & editing. FD: Writing – review & editing. MW: Funding acquisition, Project administration, Supervision, Writing – review & editing, Conceptualization.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This research was supported by a grant from the German Research Foundation (DFG, WE 4801/3-1) to MW. During the preparation of this manuscript, FD was supported by an Emanuel Donchin Professorial Scholarship in Psychology, from the University of Illinois.

Acknowledgments

We are thankful to Lisa Buchwald and Andrè Krügel for providing the data from the eye tracking experiment. We are also thankful to all research assistants involved in these projects.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2024.1459617/full#supplementary-material

References

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., and Friston, K. J. (2012). Canonical microcircuits for predictive coding. *Neuron* 76, 695–711. doi: 10.1016/j.neuron.2012.10.038

Bates, D., Mächler, M., Zurich, E., Bolker, B. M., and Walker, S. C. (2012). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Ben-Yakov, A., Smith, V., Henson, R., Aitken, F., and Kok, P. (2022). The limited reach of surprise: evidence against effects of surprise on memory for preceding elements of an event. *Psychon. Bullet. Rev.* 13, 1053–1064. doi: 10.3758/s13423-021-01954-5

Bisby, J., Horner, A., Horlyck, L., and Burgess, N. (2015). Opposing effects of negative emotion on item and associative memory are predicted by changes in amygdala and hippocampal activity. *Soc. Cogn. Affect. Neurosci.* 1, 46S—47S. doi: 10.1093/scan/nsw028

Bisby, J. A., and Burgess, N. (2014). Negative affect impairs associative memory but not item memory. *Learn. Mem.* 21, 21–27. doi: 10.1101/lm.032409.113

Boedhoe, P. S. W., Heymans, M. W., Schmaal, L., Abe, Y., Alonso, P., Ameis, S. H., et al. (2019). An empirical comparison of meta- and mega-analysis with data from the ENIGMA obsessive-compulsive disorder working group. *Front. Neuroinformat.* 12, 1–8. doi: 10.3389/fninf.2018.00102

Bogdan, P.C., Dolcos, F., Katsumi, Y., O'Brien, M., Iordan, A.D., Iwinski, S., et al. (2024). Reconciling opposing effects of emotion on relational memory: behavioral, eye-tracking, and brain imaging investigations. *J. Exp. Psychol.: Gen.* 153, 3074–3106. doi: 10.1037/xge0001625

Bogdan, P. C., Dolcos, S., Federmeier, F., Lleras, A., Schwarb, H., and Dolcos, F. (2023). Emotional dissociations in temporal associations: opposing effects of arousal on memory for details surrounding unpleasant events. *Cogn. Emot.* doi: 10.1080/02699931.2023.2270196

Bradley, M. M., Greenwald, M. K., Petry, M. C., and Lang, P. J. (1992). Remembering pictures: pleasure and arousal in memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 18, 379–390. doi: 10.1037/0278-7393.18.2.379

Brodeur, M. B., Guérard, K., and Bouras, M. (2014). Bank of standardized stimuli (BOSS) phase II: 930 new normative photos. *PLoS ONE* 9:e106953. doi: 10.1371/journal.pone.0106953

Brodeur, M. B., Kehayia, E., Dion-Lessard, G., Chauret, M., Montreuil, T., Dionne-Dostie, E., et al. (2012). The bank of standardized stimuli (BOSS): comparison between French and English norms. *Behav. Res. Methods* 1980, 961–970. doi: 10.3758/s13428-011-0184-7

Buchwald, L., Krügel, A., Ventura-Bort, C., Weymar M. (2022). *Effects of emotion on source memory: An Eye tracking study* [unpublished data].

Canli, T., Desmond, J. E., Zhao, Z., and Gabrieli, J. D. E. (2002). Sex differences in the neural basis of emotional memories. *Proc. Natl. Acad. Sci. U. S. A.* 99, 10789–10794. doi: 10.1073/pnas.162356599

Chen, F. J., and Sara, S. J. (2007). Locus coeruleus activation by foot shock or electrical stimulation inhibits amygdala neurons. *Neuroscience* 144, 472–481. doi: 10.1016/j.neuroscience.2006.09.037

Chiu, Y.-C., Dolcos, F., Gonsalves, B. D., and Cohen, N. J. (2013). On opposing effects of emotion on contextual or relational memory. *Front. Psychol.* 4, 2–5. doi: 10.3389/fpsyg.2013.00103

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* 36, 181–204. doi: 10.1017/S0140525X12000477

Clayton, E. C., and Williams, C. L. (2000). Adrenergic activation of the nucleus tractus solitarius potentiates amygdala norepinephrine release and enhances retention performance in emotionally arousing and spatial memory tasks. *Behav. Brain Res.* 112, 151–158. doi: 10.1016/S0166-4328(00)00178-9

Cook, G. I., Hicks, J. L., and Marsh, R. L. (2007). Source monitoring is not always enhanced for valenced material. *Mem. Cogn.* 35, 222–230. doi: 10.3758/BF03193443

Craik, F. I. M., and Tulving, E. (1975). Depth of processing and the retention of words. *J. Exp. Psychol.* 104, 268–294. doi: 10.1037/0096-3445.104.3.268

Cross, Z., Santamaria, A., and Kohler, M. J. (2018). Attention and emotion-enhanced memory: a systematic review and meta-analysis of behavioural and neuroimaging evidence. *bioRxiv* 2018:273920. doi: 10.1101/273920

D'Argembeau, A., and Van der Linden, M. (2005). Influence of emotion on memory for temporal information. *Emotion* 5, 503–507. doi: 10.1037/1528-3542.5.4.503

De Goede, M., and Postma, A. (2008). Gender differences in memory for objects and their locations: a study on automatic versus controlled encoding and retrieval contexts. *Brain Cogn.* 66, 232–242. doi: 10.1016/j.bandc.2007.08.004

Doerksen, S., and Shimamura, A. P. (2001). Source memory enhancement for emotional words. *Emotion* 1, 5–11. doi: 10.1037/1528-3542.1.1.5

Dolcos, F., Katsumi, Y., Moore, M., Berggren, N., de Gelder, B., Derakshan, N., et al. (2020). Neural correlates of emotion-attention interactions: from perception, learning, and memory to social cognition, individual differences, and training interventions. *Neurosci. Biobehav. Rev.* 8:17. doi: 10.1016/j.neubiorev.2019.08.017

Dolcos, F., Katsumi, Y., Weymar, M., Moore, M., Tsukiura, T., and Dolcos, S. (2017). Emerging directions in emotional episodic memory. *Front. Psychol.* 8, 1–25. doi: 10.3389/fpsyg.2017.01867

Dolcos, F., Labar, K. S., and Cabeza, R. (2004). Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory : an event-related fMRI study. *Neuroimage* 23, 64–74. doi: 10.1016/j.neuroimage.2004.05.015

Dolcos, F., LaBar, K. S., and Cabeza, R. (2005). Remembering one year later: role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proc. Natl. Acad. Sci. U. S. A.* 102, 2626–2631. doi: 10.1073/pnas.0409848102

Eichenbaum, H., Yonelinas, A. P., and Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Ann. Rev. Neurosci.* 30, 123–152. doi: 10.1146/annurev.neuro.30.051606.094328

Eldridge, L. L., Sarfatti, S., and Knowlton, B. J. (2002). The effect of testing procedure on remember-know judgments. *Psychon. Bullet. Rev.* 9, 139–145. doi: 10.3758/BF03196270

Ferré, P., Comesaña, M., and Guasch, M. (2019). Emotional content and source memory for language: impairment in an incidental encoding task. *Front. Psychol.* 10:65. doi: 10.3389/fpsyg.2019.00065

Ferreira-Santos, F. (2016). The role of arousal in predictive coding. *Behav. Brain Sci.* 39:e207. doi: 10.1017/S0140525X15001788

Friston, K. (2010). The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11, 127–138. doi: 10.1038/nrn2787

Friston, K., FitzGerald, T., Rigoli, F., Schwartenbeck, P., and Pezzulo, G. (2017). Active inference: a process theory. *Neural Comput.* 29, 1–49. doi: 10.1162/NECO_a_00912

Gardiner, J. M., Ramponi, C., and Richardson-Klavehn, A. (1998). Experiences of remembering, knowing, and guessing. *Conscious Cogn.* 26, 1–26. doi: 10.1006/ccog.1997.0321

Giraudier, M., Ventura-Bort, C., Burger, A. M., Claes, N., D'Agostini, M., Fischer, R., et al. (2022). Evidence for a modulating effect of transcutaneous auricular vagus nerve stimulation (taVNS) on salivary alpha-amylase as indirect noradrenergic marker: a pooled mega-analysis. *Brain Stimul.* 15, 1378–1388. doi: 10.1016/j.brs.2022.09.009

Graciela, J., Galindo, M., and Cansino, S. (2016). Emotional context during encoding modulates recognition electrophysiological activity. *Exp. Brain Res.* 235, 169–179. doi: 10.1007/s00221-016-4780-8

Greenland, S., Senn, S. J., Rothman, K. J., Carlin, J. B., Poole, C., Goodman, S. N., et al. (2016). Statistical tests, *P*-values, confidence intervals, and power: a guide to misinterpretations. *Eur. J. Epidemiol.* 31, 337–350. doi: 10.1007/s10654-016-0149-3

Greve, A., Cooper, E., Kaula, A., Anderson, M. C., and Henson, R. (2017). Does prediction error drive one-shot declarative learning? *J. Mem. Lang.* 94, 149–165. doi: 10.1016/j.jml.2016.11.001

Guillem, F., and Mograss, M. (2005). Gender differences in memory processing: evidence from event-related potentials to faces. *Brain Cogn.* 57, 84–92. doi: 10.1016/j.bandc.2004.08.026

Guillet, R., and Arndt, J. (2009). Taboo words: the effect of emotion on memory for peripheral information. *Mem. Cogn.* 37, 866–879. doi: 10.3758/MC.37.6.866

Guo, J., Li, D., Bi, Y., and Chen, C. (2018). Modulating effects of contextual emotions on the neural plasticity induced by word learning. *Front. Hum. Neurosci.* 12, 1–13. doi: 10.3389/fnhum.2018.00464

Hanslmayr, S., Spitzer, B., and Bäuml, K. H. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebr. Cortex* 19, 1631–1640. doi: 10.1093/cercor/bhn197

Harley, C. W. (2007). Norepinephrine and the dentate gyrus. *Progr. Brain Res.* 163, 299–318. doi: 10.1016/S0079-6123(07)63018-0

Held, L., and Ott, M. (2018). On *p*-values and bayes factors. *Ann. Rev. Stat. Appl.* 5, 393–419. doi: 10.1146/annurev-statistics-031017-100307

Henckens, M. J. A. G., Hermans, E. J., Pu, Z., and Joe, M. (2009). Stressed memories: how acute stress affects memory formation in humans. *J. Neurosci.* 29, 10111–10119. doi: 10.1523/JNEUROSCI.1184-09.2009

Henson, R. N., Campbell, K. L., Davis, S. W., Taylor, J. R., Emery, T., Erzinclioglu, S., et al. (2016). Multiple determinants of lifespan memory differences. *Sci. Rep.* 6, 1–14. doi: 10.1038/srep32527

Hicks, J. L., and Marsh, R. L. (1999). Remember-know judgments can depend on how memory is tested. *Psychon. Bullet. Rev.* 6, 117–122. doi: 10.3758/BF03210818

Hohwy, J. (2013). *The Predictive Mind.* Oxford University Press. doi: 10.1093/acprof:oso/9780199682737.001.0001

Hommel, B., Fischer, R., Colzato, L. S., Van den Wildenberg, W. P. M., and Cellini, C. (2012). The effect of fMRI (Noise) on cognitive control. *J. Exp. Psychol. Hum. Percept. Perform.* 38, 290–301. doi: 10.1037/a0026353

Hutchinson, J. B., and Barrett, L. F. (2019). The power of predictions: an emerging paradigm for psychological research. *Curr. Dir. Psychol. Sci.* 28, 280–291. doi: 10.1177/0963721419831992

Jaeger, A., Johnson, J. D., Corona, M., and Rugg, M. D. (2009). ERP correlates of the incidental retrieval of emotional information: effects of study-test delay. *Brain Res.* 1269, 105–113. doi: 10.1016/j.brainres.2009.02.082

Jaeger, A., and Rugg, M. D. (2012). Implicit effects of emotional contexts: an ERP study. *Cogn. Affect. Behav. Neurosci.* 1, 748–760. doi: 10.3758/s13415-012-0110-1

James, W. (1890). "The principles of psychology," in *Classics in Psychology*, ed. R. H. Wozniak (London: Thoemmes Continuum).

Kafkas, A., and Montaldi, D. (2018). Expectation affects learning and modulates memory experience at retrieval. *Cognition* 180, 123–134. doi: 10.1016/j.cognition.2018.07.010

Kalbe, F., and Schwabe, L. (2020). Beyond arousal: prediction error related to aversive events promotes episodic memory formation. *J. Exp. Psychol. Learn. Mem. Cogn.* 46, 234–246. doi: 10.1037/xlm0000728

Kalbe, F., and Schwabe, L. (2022). Prediction errors for aversive events shape long-term memory formation through a distinct neural mechanism. *Cerebr. Cortex* 32, 2924–2942. doi: 10.1093/cercor/bhab402

Kensinger, E. A. (2009). Remembering the details: effects of emotion. *Emot. Rev. J. Int. Soc Res. Emot*. 1, 99–113. doi: 10.1177/1754073908100432

Kensinger, E. A., Garoff-Eaton, R. J., and Schacter, D. L. (2007). Effects of emotion on memory specificity: memory trade-offs elicited by negative visually arousing stimuli. *J. Mem. Lang*. 56, 575–591. doi: 10.1016/j.jml.2006.05.004

King, D. R., de Chastelaine, M., Elward, R. L., Wang, T. H., and Rugg, M. D. (2015). Recollection-related increases in functional connectivity predict individual differences in memory accuracy. *J. Neurosci*. 35, 1763–1772. doi: 10.1523/JNEUROSCI.3219-14.2015

LaBar, K. S., and Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nat. Rev. Neurosci*. 7, 54–64. doi: 10.1038/nrn1825

Lang, P. J., Bradley, M. M., and Cuthbert, B. N. (2008). *Affective Ratings of Pictures and Instruction Manual International Affective Picture System (IAPS): Instruction Manual and Affectiv Ratings. Technical Report A-7*. The Center for Research in Psychophysiology.

Lee, K. M., Ferreira-Santos, F., and Satpute, A. B. (2021). Predictive processing models and affective neuroscience. *Neurosci. Biobehav. Rev*. 131, 211–228. doi: 10.1016/j.neubiorev.2021.09.009

Lee, M. D., and Wagenmakers, E.-J. (2013). *Bayesian Cognitive Modeling: A Practical Course (S. xiii, 264)*. Cambridge University Press. doi: 10.1017/CBO9781139087759

Lenth, R. V. (2016). Least-squares means: the R Package lsmeans. *J. Stat. Softw*. 69, 1–33. doi: 10.18637/jss.v069.i01

Luck, D., Leclerc, M.-E., and Lepage, M. (2014). The potentiation of associative memory by emotions: an event-related FMRI study. *Adv. Neurosci*. 2014, 1–9. doi: 10.1155/2014/964024

MacKenzie, G., Powell, T. F., and Donaldson, D. I. (2015). Positive emotion can protect against source memory impairment. *Cogn. Emot*. 29, 236–250. doi: 10.1080/02699931.2014.911145

Madan, C. R., Caplan, J. B., Lau, C. S. M., and Fujiwara, E. (2012). Emotional arousal does not enhance association-memory. *J. Mem. Lang*. 66, 695–716. doi: 10.1016/j.jml.2012.04.001

Madan, C. R., Fujiware, E., Caplan, J. B., and Sommer, T. (2017). Emotional arousal impairs association-memory: roles of amygdala and hippocampus. *NeuroImage* 156, 14–28. doi: 10.1016/j.neuroimage.2017.04.065

Madan, C. R., Knight, A. G., Kensinger, E. A., Steinmetz, R. M., Madan, C. R., Knight, A. G., et al. (2020). Affect enhances object-background associations: evidence from behaviour and mathematical modelling. *Cogn. Emot*. 2019, 1–10. doi: 10.1080/02699931.2019.1710110

Madan, C. R., Scott, S. M. E., and Kensinger, E. A. (2019). Positive emotion enhances association-memory. *Emotion* 19, 733–740. doi: 10.1037/emo0000465

Maddock, R. J., Garrett, A. S., and Buonocore, M. H. (2001). Remembering familiar people: the posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience* 108:7. doi: 10.1016/S0306-4522(01)00108-7

Maddock, R. J., Garrett, A. S., and Buonocore, M. H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Hum. Brain Map*. 18, 30–41. doi: 10.1002/hbm.10075

Mao, X., You, Y., Li, W., and Guo, C. (2015). Emotion impairs extrinsic source memory-an ERP study. *Biol. Psychol*. 110, 182–189. doi: 10.1016/j.biopsycho.2015.07.005

Maratos, E. J., and Rugg, M. D. (2001). Electrophysiological correlates of the retrieval of emotional and non-emotional context. *J. Cogn. Neurosci*. 13, 877–891. doi: 10.1162/089892901753165809

Mather, M., Clewett, D., Sakaki, M., and Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: how arousal amplifies selectivity in perception and memory. *Behav. Brain Sci*. 39:667. doi: 10.1017/S0140525X15000667

Mather, M., Gorlick, M. A., and Nesmith, K. (2009). The limits of arousal's memory-impairing effects on nearby information. *Am. J. Psychol*. 122, 349–369. doi: 10.2307/27784408

Mather, M., and Knight, M. (2008). The emotional Harbinger effect: poor context memory for cues that previously predicted something arousing. *Emotion* 8, 850–860. doi: 10.1037/a0014087

Mather, M., Mitchell, K. J., Raye, C. L., Novak, D. L., Greene, E. J., and Johnson, M. K. (2006). Emotional arousal can impair feature binding in working memory. *J. Cogn. Neurosci*. 4:614. doi: 10.1162/jocn.2006.18.4.614

Mather, M., and Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspect. Psychol. Sci*. 6, 114–133. doi: 10.1177/1745691611400234

McGaugh, J. L. (2000). Neuroscience - memory - a century of consolidation. *Science* 287, 248–251. doi: 10.1126/science.287.5451.248

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Ann. Rev. Neurosci*. 27, 1–28. doi: 10.1146/annurev.neuro.27.070203.144157

McIntyre, C. K., McGaugh, J. L., and Williams, C. L. (2012). Interacting brain systems modulate memory consolidation. *Neurosci. Biobehav. Rev*. 36, 1750–1762. doi: 10.1016/j.neubiorev.2011.11.001

Meaux, E., Sterpenich, V., and Vuilleumier, P. (2019). Emotional learning promotes perceptual predictions by remodeling stimulus representation in visual cortex. *Sci. Rep*. 9, 1–14. doi: 10.1038/s41598-019-52615-6

Mello-Carpes, P. B., and Izquierdo, I. (2013). The nucleus of the solitary tract→ nucleus paragigantocellularis→ locus coeruleus→ CA1 region of dorsal hippocampus pathway is important for consolidation of object recognition memory. *Neurobiol. Learn. Mem*. 100, 56–63. doi: 10.1016/j.nlm.2012.12.002

Minor, G., and Herzmann, G. (2019). Effects of negative emotion on neural correlates of item and source memory during encoding and retrieval. *Brain Res*. 1718, 32–45. doi: 10.1016/j.brainres.2019.05.001

Moreno-Martínez, F. J., and Montoro, P. R. (2012). An ecological alternative to Snodgrass and Vanderwart: 360 high quality colour images with norms for seven psycholinguistic variables. *PLoS ONE* 7, 34–42. doi: 10.1371/journal.pone.0037527

Murray, B. D., and Kensinger, E. A. (2013). A review of the neural and behavioral consequences for unitizing emotional and neutral information. *Front. Behav. Neurosci*. 7, 1–12. doi: 10.3389/fnbeh.2013.00042

Nashiro, K., and Mather, M. (2011). How arousal affects younger and older adults' memory binding. *Exp. Aging Res*. 37, 108–128. doi: 10.1080/0361073X.2011.536746

Ortiz-Tudela, J., Nolden, S., Pupillo, F., Ehrlich, I., Turan, G., and Shing, Y. L. (2021). Not what U expect: effects of prediction errors on episodic memory. *PsyArXiv* 3, 1–54. doi: 10.31234/osf.io/8dwb3

Palombo, D. J., and Cocquyt, C. (2020). Emotion in context: remembering when. *Trends Cogn. Sci*. 24, 687–690. doi: 10.1016/j.tics.2020.05.017

Pedale, T., Macaluso, E., and Santangelo, V. (2019). Enhanced insular/prefrontal connectivity when resisting from emotional distraction during visual search. *Brain Struct. Funct*. 224, 2009–2026. doi: 10.1007/s00429-019-01873-1

Pierce, B. H., and Kensinger, E. A. (2011). Effects of emotion on associative recognition: valence and retention interval matter. *Emotion* 11, 139–144. doi: 10.1037/a0021287

Plessow, F., Fischer, R., Kirschbaum, C., and Goschke, T. (2011). Inflexibly focused under stress: acute psychosocial stress increases shielding of action goals at the expense of reduced cognitive flexibility with increasing time lag to the stressor. *J. Cogn. Neurosci*. 23, 3218–3227. doi: 10.1162/jocn_a_00024

Quent, J. A., Greve, A., and Henson, R. N. (2022). Shape of U: the nonmonotonic relationship between object-location memory and expectedness. *Psychol. Sci*. 33, 2084–2097. doi: 10.1177/09567976221109134

Ranganath, C. (2010). Binding items and contexts: the cognitive neuroscience of episodic memory. *Curr. Direct. Psychol. Sci*. 19, 131–137. doi: 10.1177/0963721410368805

Ranganath, C., and Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nat. Rev. Neurosci*. 13, 713–726. doi: 10.1038/nrn3338

Rao, R. P. N., and Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat. Neurosci*. 2, 79–87. doi: 10.1038/4580

Rhodes, S., Greene, N. R., and Naveh-Benjamin, M. (2019). Age-related differences in recall and recognition: a meta-analysis. *Psychon. Bullet. Rev*. 26, 1529–1547. doi: 10.3758/s13423-019-01649-y

Rimmele, U., Davachi, L., Petrov, R., Dougal, S., and Phelps, E. A. (2011). Emotion enhances the subjective feeling of remembering, despite lower accuracy for contextual details. *Emotion* 11, 553–562. doi: 10.1037/a0024246

Rimmele, U., Davachi, L., and Phelps, E. A. (2012). Memory for time and place contributes to enhanced confidence in memories for emotional events. *Emotion* 12, 834–846. doi: 10.1037/a0028003

Ritchey, M., Dolcos, F., and Cabeza, R. (2008). Role of amygdala connectivity in the persistence of emotional memories over time: an event-related fMRI investigation. *Cerebr. Cortex* 18, 2494–2504. doi: 10.1093/cercor/bhm262

Rouhani, N., Niv, Y., Frank, M. J., and Schwabe, L. (2023). Multiple routes to enhanced memory for emotionally relevant events. *Trends Cogn. Sci*. 27, 867–882. doi: 10.1016/j.tics.2023.06.006

Rugg, M. D., and Vilberg, K. L. (2013). Brain networks underlying episodic memory retrieval. *Curr. Opin. Neurobiol*. 23, 255–260. doi: 10.1016/j.conb.2012.11.005

Salsano, I., Tain, R., Giulietti, G., Williams, D. P., Ottaviani, C., Antonucci, G., et al. (2024). Negative emotions enhance memory-guided attention in a visual search task by increasing frontoparietal, insular, and parahippocampal cortical activity. *Cortex* 173, 16–33. doi: 10.1016/j.cortex.2023.12.014

Schiller, D., Yu, A. N. C., Alia-Klein, N., Becker, S., Cromwell, H. C., Dolcos, F., et al. (2023). The human affectome. *Neurosci. Biobehav. Rev*. 158:105450. doi: 10.1016/j.neubiorev.2023.105450

Schümann, D., Bayer, J., Talmi, D., and Sommer, T. (2017). Dissociation of immediate and delayed effects of emotional arousal on episodic memory. *Neurobiol. Learn. Mem*. 148, 11–19. doi: 10.1016/j.nlm.2017.12.007

Schwabe, L. (2017). Memory under stress: from single systems to network changes. *Eur. J. Neurosci*. 45, 478–489. doi: 10.1111/ejn.13478

Schwabe, L., Haddad, L., and Schachinger, H. (2008). HPA axis activation by a socially evaluated cold-pressor test. *Psychoneuroendocrinology* 33, 890–895. doi: 10.1016/j.psyneuen.2008.03.001

Schwabe, L., Hermans, E. J., Joëls, M., and Roozendaal, B. (2022). Mechanisms of memory under stress. *Neuron* 110, 1450–1467. doi: 10.1016/j.neuron.2022.02.020

Schwabe, L., Nader, K., and Pruessner, J. C. (2013). β-Adrenergic blockade during reactivation reduces the subjective feeling of remembering associated with emotional episodic memories. *Biol. Psychol.* 92, 227–232. doi: 10.1016/j.biopsycho.2012.10.003

Schwabe, L., and Schächinger, H. (2018). Ten years of research with the Socially Evaluated Cold Pressor Test: data from the past and guidelines for the future. *Psychoneuroendocrinology* 92, 155–161. doi: 10.1016/j.psyneuen.2018.03.010

Schwartz, R. M. (1997). Consider the simple screw: cognitive science, quality improvement, and psychotherapy. *J. Consult. Clin. Psychol.* 65, 970–983. doi: 10.1037/0022-006x.65.6.970

Schwartz, R. M., Reynolds III, C. F., Thase, M. E., Frank, E., Fasiczka, A. L., and Haaga, D. A. F. (2002). Optimal and normal affect balance in psychotherapy of major depression: evaluation of the balanced states of mind model. *Behav. Cogn. Psychother.* 30, 439–450. doi: 10.1017/S1352465802004058

Segal, S. K., and Cahill, L. (2009). Endogenous noradrenergic activation and memory for emotional material in men and women. *Psychoneuroendocrinology* 34, 1263–1271. doi: 10.1016/j.psyneuen.2009.04.020

Sharot, T., Delgado, M. R., and Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nat. Neurosci.* 7, 1376–1380. doi: 10.1038/nn1353

Sharot, T., and Yonelinas, A. P. (2008). Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition* 106, 538–547. doi: 10.1016/j.cognition.2007.03.002

Smeets, T., Cornelisse, S., Quaedflieg, C. W. E. M., Meyer, T., Jelicic, M., and Merckelbach, H. (2012). Introducing the Maastricht Acute Stress Test (MAST): a quick and non-invasive approach to elicit robust autonomic and glucocorticoid stress responses. *Psychoneuroendocrinology* 37, 1998–2008. doi: 10.1016/j.psyneuen.2012.04.012

Smith, A. P. R., Henson, R. N., A., Rugg, M. D., and Dolan, R. J. (2005). Modulation of retrieval processing reflects accuracy of emotional source memory. *Learn. Mem.* 12, 472–479. doi: 10.1101/lm.84305

Smith, A. P. R., Henson, R. N. A., Dolan, R. J., and Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *NeuroImage* 22, 868–878. doi: 10.1016/j.neuroimage.2004.01.049

Squire, L. R., Wixted, J. T., and Clark, R. E. (2007). Recognition memory and the medial temporal lobe: a new perspective. *Nat. Rev. Neurosci.* 8, 872–883. doi: 10.1038/nrn2154

Sterling, P., and Laughlin, S. (2015). *Principles of Neural Design.* The MIT Press. doi: 10.7551/mitpress/9780262028707.001.0001

Strange, B. A., and Dolan, R. J. (2004). Beta-adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. *Proc. Natl. Acad. Sci. U. S. A.* 101, 11454–11458. doi: 10.1073/pnas.0404282101

Strube, A., Rose, M., Fazeli, S., and Büchel, C. (2021). Alpha-to-beta- and gamma-band activity reflect predictive coding in affective visual processing. *Sci. Rep.* 11, 1–16. doi: 10.1038/s41598-021-02939-z

Tessner, K. D., Walker, E. F., Hochman, K., and Hamann, S. (2006). Cortisol responses of healthy volunteers undergoing magnetic resonance imaging. *Hum. Brain Mapp.* 27, 889–895. doi: 10.1002/hbm.20229

Touryan, S. R., Marian, D. E., and Shimamura, A. P. (2007). Effect of negative emotional pictures on associative memory for peripheral information. *Memory* 15, 154–166. doi: 10.1080/09658210601151310

Tukey, J. W. (1949). Comparing individual means in the analysis of variance. *Biometrics* 5, 99–114. doi: 10.2307/3001913

Tulving, E. (1985). Memory and consciousness. *Can. Psychol.* 26, 1–12. doi: 10.1037/h0080017

Van Kesteren, M. T. R., Ruiter, D. J., Fernández, G., and Henson, R. N. (2012). How schema and novelty augment memory formation. *Trends Neurosci.* 35, 211–219. doi: 10.1016/j.tins.2012.02.001

Ventura-Bort, C., Dolcos, F., Wendt, J., Wirkner, J., Hamm, A. O., and Weymar, M. (2020a). Item and source memory for emotional associates is mediated by different retrieval processes. *Neuropsychologia* 145, 12–15. doi: 10.1016/j.neuropsychologia.2017.12.015

Ventura-Bort, C., Löw, A., Wendt, J., Dolcos, F., Hamm, A. O., and Weymar, M. (2016a). When neutral turns significant: brain dynamics of rapidly formed associations between neutral stimuli and emotional contexts. *Eur. J. Neurosci.* 44, 2176–2183. doi: 10.1111/ejn.13319

Ventura-Bort, C., Löw, A., Wendt, J., Moltó, J., Poy, R., Dolcos, F., et al. (2016b). Binding neutral information to emotional contexts: brain dynamics of recognition after a long retention interval. *Cogn. Affect. Behav. Neurosci.* 16, 234–247. doi: 10.3758/s13415-015-0385-0

Ventura-Bort, C., Wendt, J., Wirkner, J., König, J., Lotze, M., Hamm, A. O., et al. (2020b). Neural substrates of long-term item and source memory for emotional associates: an fMRI study. *Neuropsychologia* 147:107561. doi: 10.1016/j.neuropsychologia.2020.107561

Ventura-Bort, C., Wirkner, J., Dolcos, F., Wendt, J., Hamm, A. O., and Weymar, M. (2019a). Enhanced spontaneous retrieval of cues from emotional events: an ERP study. *Biol. Psychol.* 148:107742. doi: 10.1016/j.biopsycho.2019.107742

Ventura-Bort, C., Wirkner, J., Hamm O. A., and Weymar M. (2019b). *Effects of Immediate and Delayed Acute Stress on Emotional Source Memory: an ERP Study* [unpublished data].

Ventura-Bort, C., Wirkner, J., Wendt, J., Hamm, A. O., and Weymar, M. (2021). Establishment of emotional memories is mediated by vagal nerve activation: evidence from noninvasive taVNS. *J. Neurosci.* 41, 7636–7648. doi: 10.1523/JNEUROSCI.2329-20.2021

Ventura-Bort, C., Wirkner, J., Wendt, J., Schwabe, L., Dolcos, F., Hamm, A. O., et al. (2024). Opposing effects of pre-encoding stress on neural substrates of item and emotional contextual source memory retrieval. *Neurobiol. Stress* 33:100691. doi: 10.1016/j.ynstr.2024.100691

Wagenmakers, E. J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Love, J., et al. (2018). Bayesian inference for psychology. Part I: theoretical advantages and practical ramifications. *Psychon. Bullet. Rev.* 25, 35–57. doi: 10.3758/s13423-017-1343-3

Wagner, H. L. (1993). On measuring performance in category judment studies of nonverbal behavior. *J. Nonverb. Behav.* 17:3. doi: 10.1007/BF00987006

Weymar, M., and Hamm, A. (2013). Electrophysiological signature of emotional memories. *Hurt. Mem. Benef. Forget.* 2, 21–35. doi: 10.1016/B978-0-12-398393-0.00002-X

Weymar, M., Löw, A., and Hamm, A. O. (2011). Emotional memories are resilient to time: evidence from the parietal ERP old/new effect. *Hum. Brain Map.* 32, 632–640. doi: 10.1002/hbm.21051

Weymar, M., Löw, A., Melzig, C. A., and Hamm, A. O. (2009). Enhanced long-term recollection for emotional pictures: evidence from high-density ERPs. *Psychophysiology* 46, 1200–1207. doi: 10.1111/j.1469-8986.2009.00869.x

Weymar, M., Löw, A., Modess, C., Engel, G., Gründling, M., Petersmann, A., et al. (2010). Propranolol selectively blocks the enhanced parietal old/new effect during long-term recollection of unpleasant pictures: a high density ERP study. *NeuroImage* 49, 2800–2806. doi: 10.1016/j.neuroimage.2009.10.025

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., et al. (2019). Welcome to the Tidyverse. *J. Open Source Softw.* 4:1686. doi: 10.21105/joss.01686

Williams, C. L., Men, D., Clayton, E. C., and Gold, P. E. (1998). Norepinephrine release in the amygdala after systemic injection of epinephrine or escapable footshock: contribution of the nucleus of the solitary tract. *Behav. Neurosci.* 112, 1414–1422. doi: 10.1037/0735-7044.112.6.1414

Williams, S. E., Ford, J. H., and Kensinger, E. A. (2022). The power of negative and positive episodic memories. *Cogn. Affect. Behav. Neurosci.* 22, 869–903. doi: 10.3758/s13415-022-01013-z

Wirkner, J., Ventura-Bort, C., Hamm O. A., and Weymar, M. (2015). *Effects of Immediate Acute Stress on Emotional Source Memory: an ERP Study* [unpublished data].

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *J. Mem. Lang.* 46, 441–517. doi: 10.1006/jmla.2002.2864

Yonelinas, A. P., and Jacoby, L. L. (1995). The relation between remembering and knowing as bases for recognition: effects of size congruency. *J. Mem. Lang.* 34, 622–643. doi: 10.1006/jmla.1995.1028

Yonelinas, A. P., Kroll, N. E. A., Quamme, J. R., Lazzara, M. M., Sauvé, M. J., Widaman, K. F., et al. (2002). Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nat. Neurosci.* 5, 1236–1241. doi: 10.1038/nn961

frontiers | Frontiers in Psychology

TYPE Review
PUBLISHED 14 May 2025
DOI 10.3389/fpsyg.2025.1483373

OPEN ACCESS

EDITED BY
Hadas Okon-Singer,
University of Haifa, Israel

REVIEWED BY
Giovanni Mirabella,
University of Brescia, Italy
Christopher Brown,
Bournemouth University, United Kingdom

*CORRESPONDENCE
Florin Dolcos
✉ fdolcos@illinois.edu
Sanda Dolcos
✉ sdolcos@illinois.edu

RECEIVED 19 August 2024
ACCEPTED 28 January 2025
PUBLISHED 14 May 2025

CITATION
Dolcos F, Denkova E, Iordan AD, Shafer AT, Fernández G and Dolcos S (2025) Dissociating and linking divergent effects of emotion on cognition: insights from current research and emerging directions.
Front. Psychol. 16:1483373.
doi: 10.3389/fpsyg.2025.1483373

Dissociating and linking divergent effects of emotion on cognition: insights from current research and emerging directions

Florin Dolcos[1,2,3]*, Ekaterina Denkova[4], Alexandru D. Iordan[2,3,5], Andrea T. Shafer[6], Guillén Fernández[7] and Sanda Dolcos[1,2,3]*

[1]Department of Psychology, University of Illinois, Urbana-Champaign, IL, United States, [2]Neuroscience Program, University of Illinois, Urbana-Champaign, IL, United States, [3]Beckman Institute for Advanced Science and Technology, University of Illinois, Urbana-Champaign, IL, United States, [4]Department of Psychology, University of Miami, Coral Gables, FL, United States, [5]Department of Psychology, University of Michigan, Ann Arbor, MI, United States, [6]Centre for Neuroscience, University of Alberta, Edmonton, AB, Canada, [7]Donders Institute for Brain, Cognition, and Behaviour, Radboud University Medical Center, Nijmegen, Netherlands

This century has witnessed unprecedented increasing interest in the investigation of emotion-cognition interactions and the associated neural mechanisms. The present review emphasizes the need to consider the various factors that can influence enhancing and impairing effects of emotion on cognition, in studies of both healthy and clinical groups. First, we discuss advances in understanding the circumstances in which emotion enhances or impairs cognition at different levels, both *within the same processes* (e.g., perception, episodic memory) and *across different processes* (i.e., episodic vs. working memory). Then, we discuss evidence regarding these opposing effects of emotion in a larger context, of the *response to stressors,* and linked to the role of individual differences (personality, genetic) affecting stress sensitivity. Finally, we also discuss evidence linking these opposing effects of emotion in a *clinical group* (PTSD), where they are both deleterious, and based on comparisons *across groups* with opposing affective biases: healthy aging (*positive bias*) vs. depression (*negative bias*). These issues have relevance for understanding mechanisms of emotion-cognition interactions in healthy functioning and in psychopathology, which can inspire training interventions to increase resilience and well-being.

KEYWORDS

attention, emotional memory, working memory, emotional distraction, emotion perception, stress, cognitive aging, affective disorders

1 Introduction

Emotion can enhance or hinder various aspects of our cognition and behavior. For instance, the emotional charge of an event can increase attention to and memory for that event, leading to enhanced memory, whereas task-irrelevant emotional information may lead to increased distraction and hence can impair cognitive performance. The overarching goal of this review is to discuss evidence regarding factors that influence opposing effects of emotion on cognitive processing at different levels (Figure 1), and the associated neural mechanisms, and to highlight the need to consider such factors in studies investigating emotion-cognition interactions in healthy and clinical groups. These issues have relevance for understanding mechanisms of emotion-cognition interactions in healthy functioning and in emotional disturbances, where such opposing effects[1] of emotion tend to be exacerbated and deleterious. Notably, we do not aim to present the available evidence regarding the impact of emotion on different aspects of cognition as part of a coherent theoretical framework. The main rationale for our approach is to increase awareness of the fact that such effects can occur and be identified at different levels. This is because the tendency is to be treated in isolation, in separate literatures (e.g., attention, perception, memory). Hence, the present review provides a more comprehensive image of these divergent effects and of their possible links.

The basic idea that emotion can have divergent effects on different cognitive aspects is not completely novel. Instead, what is novel is identification and consideration of such effects at different levels. Our first attempt to increase awareness about this goes back more than 10 years ago, when we organized a Frontiers Special Issue/Research Topic (the first in the *Emotion Science* section) tackling for the first time this matter in a comprehensive way. Our initiative was very well received and has resulted in a collection of 60+ manuscripts, received from a large number of outstanding contributors (200+, in total), pointing to divergent patters in a variety of aspects. Summarized in an Editorial and compiled in an edited book (Dolcos et al., 2015, respectively), our special issue has been at the top of popularity among the Frontiers Research Topics. Importantly, by all accounts, our initiative was very successful in increasing awareness of such patterns in the impact of emotion on cognition.

The efforts to increase awareness have contributed to further clarification of the circumstances in which emotion enhances or impairs cognition and prepared the ground for further theoretical advancements. A concrete example, which we are also highlighting here, is the recent reconciliation of evidence regarding opposing effects of emotion on relational memory (Bogdan et al., 2024). Initially, a pattern was emerging in the emotional memory literature, whereby the enhancing effects of emotion were not systematically observed in all aspects of memory (e.g., central vs. peripheral; Kensinger, 2009). Then, more recently, evidence pointed to opposing effects of emotion on item (what) vs. relational memory (item-context associations), whereby emotion enhanced item memory but impaired memory for item-context associations (Bisby and Burgess, 2017). However, we recently provided further evidence regarding the circumstances in which emotion enhances or impairs relational memory, and proposed a new theoretical account (Bogdan et al., 2024). It should be noted that, although there are various accounts proposing to explain the impact of emotion on episodic memory, no single theory covers all aspects of emotion-memory interactions. In section 2.2.4, we illustrate the difficulty in reaching a comprehensive theoretical account, even within the same domain (Figure 4), which makes it even more difficult identification of a coherent theoretical framework that covers all levels of emotion-cognition interactions. Hence the present goal of increasing awareness that such divergent patterns can be identified at different levels, while also pointing to emerging theoretical accounts resulted from research aimed at further understanding these divergent patterns in specific domains (see Figure 6, which introduces a new model of emotion-memory interactions).

Ten years after the conclusion of our special issue focusing on these aspects (Dolcos et al., 2015), many topics are still current. Below, we will briefly introduce and then discuss them in detail. First, enhancing and impairing effects of emotion can be identified *within the same cognitive processes/domains*, such as perception and episodic memory (i.e., memory for specific personal events). Opposing effects of emotion in perception can be identified linked to the context in which emotional information is processed (goal-relevant or irrelevant) (Ohman et al., 2001a; Ohman et al., 2001b), linked to the timing of its processing (simultaneous or asynchronous) (Bocanegra and Zeelenberg, 2009a, 2011b; Ciesielski et al., 2010; McHugo et al., 2013; Ohman et al., 2001a; Phelps et al., 2006), and linked to the spatial frequency of visual information (high or low spatial frequency) (Bocanegra and Zeelenberg, 2009b, 2011a; Vuilleumier et al., 2003). Regarding episodic memory, opposing effects of emotion can be attributed to different accounts, including central vs. peripheral effects (Kensinger, 2009) and high vs. low prioritization of information (Mather and Sutherland, 2011). Moreover, an important topic of research in this area concerns opposing effects of emotion on associative or relational memory (Chiu et al., 2013), which may be differentially affected in both healthy functioning and clinical condition, including neurological (Alzheimer's), affective (mood and anxiety disorders), and other disturbances (schizophrenia).

Second, there is also emerging evidence of opposing effects of emotion *across cognitive processes/domains*, which also emphasizes the link and dissociation between immediate and long-term effects of emotional distraction on perception and working memory (Dolcos, 2013; Shafer and Dolcos, 2012), on the one hand, and episodic memory, on the other hand. For instance, task-irrelevant emotional information can impair ongoing cognitive processing, while also enhancing long-term memory for the distracters themselves. Seeing the scene of a tragic accident while driving may temporarily distract us from the main task (driving), while also leading to better memory for the distracting information (the totaled cars). Novel brain imaging evidence regarding these phenomena points to both overlapping and dissociable neural mechanisms mediating these opposing effects of

---

[1] *Enhancing* vs. *impairing* effects of emotion may be associated with *beneficial* vs. *detrimental* effects, respectively, and hence to some extent these notions can be used interchangeably. However, this is not always the case, as dissociations can also be identified. For instance, attending to task-irrelevant emotional distraction may impair performance in cognitive tasks at hand. However, from an evolutionary perspective, having in place neural systems sensitive to emotional information whose detection and processing is relevant for survival (e.g., in threatening situations) is adaptive and hence beneficial. Therefore, the *impairing* effects of emotional distraction may be seen as "necessary side-effects" (or by-products) of *enhancing* effects of emotion on attention and perception, which overall are beneficial for survival. In the case of psychopathology, on the other hand, exacerbation of both enhancing and impairing effects of emotion are context inappropriate and thus indeed detrimental. Specifically, at a basic level, enhanced emotional memory retrieval is beneficial for survival, if it helps us predict/avoid dangerous situations. However, if it causes suffering, such as in the case of PTSD patients, who may inappropriately re-experience memories for traumatic events in actually safe situations, such enhanced memory is maladaptive and hence deleterious. This clarification is important, because a rigid view that impairing effects of emotion (or stress for that matter) on cognition are always detrimental hampers research progress. Hence, in the present discussion, *enhancing*/*impairing* effects refer to the impact of emotion on the cognitive processes or performance measures of interest (perception, memory, etc.), rather than to *beneficial*/*detrimental* effects in general, or from an evolutionary standpoint.

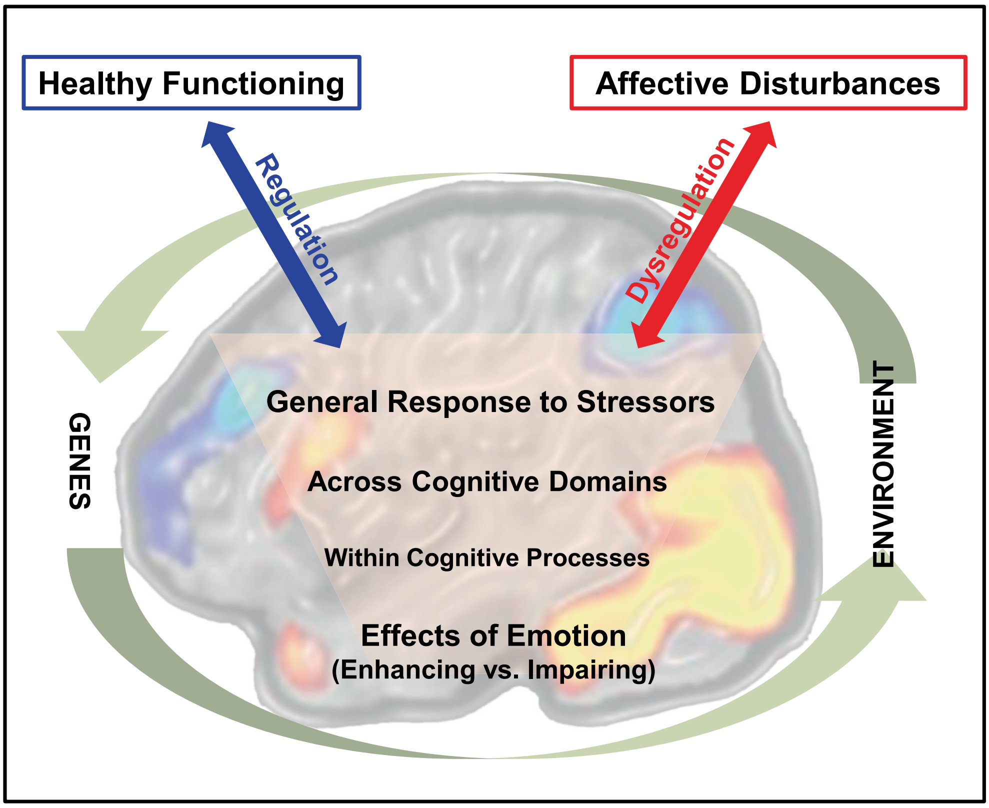


FIGURE 1
Emotion-cognition interactions in the brain and their relation to adaptive and maladaptive outcomes. The diagram illustrates opposing effects of emotion on cognition at increasing levels of complexity in emotion-cognition interactions. The involvement of brain mechanisms at all these levels is suggested by the background brain image depicting activations in brain regions that are part of two main neural systems: a dorsal neural system involved in "cold" cognitive/executive processing (illustrated by cold-colored brain activations) and a ventral system involved in "hot" emotion processing (illustrated by warm-colored brain activations). The effective vs. dysfunctional engagement of regulatory mechanisms in emotion-cognition interactions are depicted by the blue and red arrows, linked to adaptive vs. maladaptive outcomes, respectively. Finally, these interactions occur in the larger context circumscribed by interplays between genetic and environmental factors influencing them. It should be noted that the latter interplays are indirect, as genes do not affect directly our environment and the environment does not actually affect our genetic code. Instead, the genes making up the genetic code (genotype) are expressed in phenotypes that affect the environment, which in turn affects transcription and gene expression (epigenetics). The brain image was adapted from Dolcos and McCarthy (2006), with permission.

emotion (Dolcos et al., 2013; Shafer and Dolcos, 2012), and highlights the role of other factors, such as the load of the main cognitive task (Shafer and Dolcos, 2012; Shafer et al., 2012).

Third, in a *larger context of the stress response,* emotional stressors can lead to opposing effects depending on the context and degree. Optimal levels of stress may temporarily increase cognitive performance (e.g., nervousness about an upcoming important exam may motivate us to study harder), whereas high levels of stress can impair performance (e.g., overwhelming worry in the anticipation of, or during, a difficult exam may impair our ability to stay focused and perform optimally) (Diamond et al., 2007). Moreover, chronic and/or extreme levels of stress can lead to clinical conditions (Arnsten, 2009; Roozendaal et al., 2009), such as post-traumatic stress disorder (PTSD), which are associated with longer-lasting cognitive impairments. An interesting emerging finding in this area points to the role of subjective or objective control upon stressful situations (Henderson et al., 2012; Kerr et al., 2012; Mereu and Lleras, 2013), in determining the beneficial or detrimental impact on cognitive processing. In addition, recent research is also considering the role of individual differences in response to stressors, which can lead to adaptive or *mal*adaptive consequences. Thus, it is important to consider both factors related to the stressors themselves and factors related to variations (personality, genetic) in the individuals' responses to stressful situations.

Fourth, the co-occurrence of enhancing and impairing effects of emotion is probably most evident in *affective disturbances*, such as PTSD, which are characterized by increased sensitivity to emotional distraction and impaired cognitive control (Hayes et al., 2012). Thus, both of these opposing effects of emotion are exacerbated and deleterious. For example, uncontrolled recollection of traumatic memories in PTSD may interfere with ongoing cognitive processing. Evidence from PTSD studies points to altered interactions between the mechanisms that are typically responsible for enhancing vs. impairing effects of emotion in healthy functioning (Dolcos, 2013). Specifically, as discussed in Section 5, there is evidence suggesting that non-specific responses to cues for trauma-related memories, presented as task-irrelevant distraction (Morey et al., 2009), may reflect non-specific initial encoding of decontextualized memories for the traumatic events due to heightened arousal (Hayes et al., 2011).

Finally, there is also intriguing converging evidence from *across-fields comparisons* of findings from groups with opposing emotional biases, such as healthy aging (showing a positive bias, Mather, 2012;

Mather and Carstensen, 2005) vs. depression (showing a negative bias). Interestingly, these opposing biases are linked to opposite effects on the ability to control emotions in these groups – enhanced emotion regulation in healthy aging (Mather, 2012; St Jacques et al., 2010; Dolcos et al., 2014) vs. impaired emotion control or emotion *dys*regulation in depression (Mayberg, 1997). Thus, direct comparisons of these groups with opposing emotional biases and emotion regulation abilities, along with studies aiming at elucidating the mechanisms of enhanced emotional resilience in healthy aging, provide an exciting possible research avenue to address mental health issues. All these issues will be discussed in detail in the next sections. The review ends with concluding remarks and a discussion of open issues and future directions.

2 Opposing effects of emotion within the same cognitive domain

The findings discussed in this and the next section are based mainly on manipulations of transient emotional responses, which typically elicit phasic influences on cognitive processing, and we only briefly reference tonic effects of longer-lasting emotional states, such as mood and stress. Complementing this body of evidence, Section 4 specifically focuses on the impact of stress on cognitive processing. Of note, emotional reactions and states are separable phenomena, with the former being relatively more intense and short in duration and the latter being relatively more diffuse and prolonged, and they may exert different influences on cognition and behavior (Olsson and Öhman, 2009; Rottenberg and Gross, 2003; Watson, 2000).

2.1 Opposing effects of emotion on visual perception and attention

Investigation of the impact of emotion on visual perception and attention has shown that visual processing of affective information is prioritized over non-affective information. Evidence for this prioritization is provided by research using detection, visual search, attentional capture, and attentional blink paradigms. Human and non-human primate investigations of emotion processing have provided evidence that the impact of emotion on visual perception and attention is largely linked to the amygdala (AMY) (Anderson and Phelps, 2001; Lim et al., 2009; Phelps, 2006). While the routes by which AMY influences processing in sensory cortices to alter stimulus processing in the human brain remain debated (see Pessoa, 2013, for a review), both human lesion and neuroimaging data show that this brain region plays a pivotal role in low-level perceptual and attentional modulations by emotion (Anderson and Phelps, 2001; Lim et al., 2009). Evidence from studies investigating the effect of prioritization of emotion processing show that emotion can both impair and enhance performance, but the directionality of these effects depends on a number of factors. Below we will discuss evidence regarding the role of the following three aspects in determining enhancing or impairing effects of emotion on visual perception and attention: (1) the *context* of emotion processing (*task-relevant vs. irrelevant*), (2) the *timing* of emotion processing (*simultaneous vs. asynchronous*), and (3) the spatial frequency of visual emotional information (*low vs. high spatial frequency*).

2.1.1 Context of emotion processing (task-relevant vs. task-irrelevant)

An important factor in determining the impact of emotion on perception and attention is whether emotional stimuli serve as targets (task-relevant) or distracters (task-irrelevant). Rapid serial visual presentation paradigms (RSVP) and the attentional blink phenomenon (Dux and Marois, 2009; Raymond et al., 1992) offer good examples of how altering the context of emotion processing results in a different impact of emotion on behavior. In RSVP studies, streams of stimuli (words or pictures) are presented in a rapid succession, with individual stimuli presented one at a time, typically displayed for 80–125 ms each and with no interstimulus interval (ISI). In such paradigms, a so-called *attentional blink* occurs when the processing of an initial target stimulus (T1) presented in the stimulus stream impairs the ability to detect another target stimulus (T2) that is presented soon after the first target stimulus. Interestingly, when T1 is emotional, and no report of T1 is required, T1 becomes a "distracter" stimulus, and the time interval during which the ability to detect T2 becomes longer (i.e., the "blink") (McHugo et al., 2013). This is also referred to as "emotion-induced blindness" (Most et al., 2005). However, when T2 is emotional, the ability to accurately detect T2 is enhanced and the duration of the "blink" produced by processing T1 is reduced (Keil and Ihssen, 2004).

This example emphasizes a generalization that can be made about the effect of emotion on perception and attention. When an exogenous emotional stimulus is task-relevant, the prioritization of processing for affective information results in task-enhancement, whereas when task-irrelevant, the boost in processing resources received by the now distracting emotional stimulus depletes the resources available for initial or continued processing of a target stimulus. These opposing effects observed behaviorally seem to be linked to the same neural mechanisms that allow increased mobilization and allocation of processing resources associated with the prioritization of affective information and involve AMY.

2.1.2 The timing of emotion processing (simultaneous vs. asynchronous)

A related factor that influences the effects of emotion on perception and attention is the timing of presenting emotional and non-emotional stimuli. There are predominantly two main ways in which tasks are designed to examine the impact of emotion on perception and attention. In one approach, emotional stimuli are (i) presented *simultaneously* with other stimuli, whereas in the other emotional and non-emotional stimuli are presented *asynchronously* and are either (ii) distributed evenly across the screen or are (iii) limited to specific screen locations. Each of these approaches can result in either an impairing or enhancing effect of emotion on perception and attention, in relationship to the factor described above – i.e., whether the emotional information is task-relevant or not.

An example of the first approach (i) is the pop-out visual search, where emotional stimuli serve as either targets (task-relevant) or distracters (task-irrelevant). In pop-out visual search, a number of items are displayed at the same time, with all items, but one, identical. The non-identical item differs from the identical items to a degree that makes it easily identifiable and is, therefore, said to "pop-out" of the display. As highlighted above, when an emotional item is presented as target, the time required to detect it is reduced. Alternatively, when emotion is presented as distraction, the time required to detect a non-emotional target is impaired (Ohman et al., 2001b). Therefore,

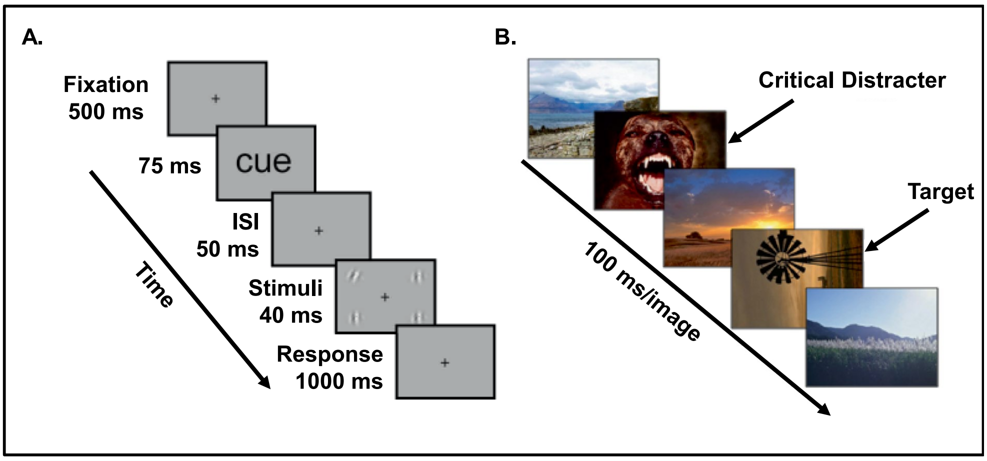


FIGURE 2
Experimental paradigms used to investigate the link between the timing of emotion processing and opposing effects of emotion on visual perception. **(A)** A briefly presented emotional cue (e.g., fearful face) enhances visual processing of neutral targets (e.g., low-contrast gratings) following a short interval (50 ms), resulting in reduced threshold of detecting the orientation of the neutral targets. From Phelps et al. (2006), with permission. **(B)** Emotional distracters impair visual processing of neutral target following a longer interval (100 ms), thus resulting in impaired ability to identify a neutral target. Notably, this impairment progressively diminishes as the time interval between the emotional stimulus and the neutral target is increased and, ultimately, identification of a neutral target is again enhanced by emotion. From Ciesielski et al. (2010), with permission.

when emotion is presented simultaneously with non-emotional items, the direction of emotion's impact will also be dependent on whether the emotional stimulus is the target (task-relevant) or serves as distraction (task-irrelevant).

Converging findings from investigations that incorporate asynchronous presentation of emotional and non-emotional items shows that differences in the stimulus duration and the length of the interstimulus interval (ISI) determine whether task-irrelevant emotional information enhances or impairs performance of an asynchronously presented non-emotional target. For example, in the case of (ii), briefly presented and distributed fear stimuli with a short ISI between the fear stimulus and a non-emotional target stimulus facilitate the perceptual processing of the non-emotional target and therefore enhance performance (Bocanegra and Zeelenberg, 2009b, 2011a; Phelps et al., 2006). Moreover, in the case of (iii), if fear stimuli also serve as spatial cues for the location of subsequent non-emotional targets, the affective and attentional information of the cue interact to boost perceptual processing of the non-emotional target even further (Figure 2A) (Phelps et al., 2006).

Interactions between the timing of presenting emotional stimuli and manipulations of their task-relevance can also be influenced by variations in the duration of the interval between an emotional stimulus and a target stimulus. For instance, in the context of the findings regarding the attentional blink discussed above, if the stimulus duration for an emotional item and the interval between an emotional item and a target item are longer, then the perceptual processing is impaired (Figure 2B) (Ciesielski et al., 2010; McHugo et al., 2013). However, if the interval is extended even further (i.e., after the attentional blink period), then emotion again shows an enhancing effect on target detection (Bocanegra and Zeelenberg, 2009a; Ciesielski et al., 2010). Consequently, when emotion is task-irrelevant but presented briefly and immediately prior to a non-emotional target, the non-emotional target receives a boost in processing and performance is enhanced. However, if more in-depth processing of task-irrelevant processing is allowed to occur, as a result of longer stimulus durations, and the target has as larger temporal gap separating it from the task-irrelevant emotion, the processing resources available to detect the non-emotional target are depleted and hence performance is impaired. Importantly, however, this impairment is only momentary and non-emotional targets presented immediately after the "blink" period also receive a boost in processing resources and performance is enhanced.

The differential impact of emotion depending on the temporal delay between emotional stimuli and non-emotional targets may, at least in-part, be explained by the time course of emotion-attention interactions on visual processing, and also involves AMY. For instance, investigations exploring the temporal aspects of emotion and attention on visual processing of task-irrelevant emotional information in the AMY, under different conditions of attentional demand in the main task (low vs. high demand), have shown differences in the susceptibility of the AMY response to affective and attentional information, over the time course of the response epoch (Luo et al., 2010; Pourtois et al., 2010). Specifically, the initial modulation occurring early in the time course was due to emotion and was invariant to the attention demands of the main task. In contrast, the later modulation was sensitive to the interaction between the emotion and attentional demands, such that an emotion response was found only when the task demands were low (Luo et al., 2010) or the emotional stimuli were task-relevant (Pourtois et al., 2010).

Regarding the neural mechanisms, the enhancement in target detection immediately following an emotional stimulus (Bocanegra and Zeelenberg, 2009b, 2011a, 2011b; Phelps et al., 2006) could result from an early, attention invariant, emotional response in the AMY, whereas the subsequent impairment in target detection could result from the later dampening of the AMY's response to emotion by concurrent attentional demands, coupled with the possibility that continued higher-ordered processing of the emotional stimulus diminishes the resources available for later perceptual processing of a

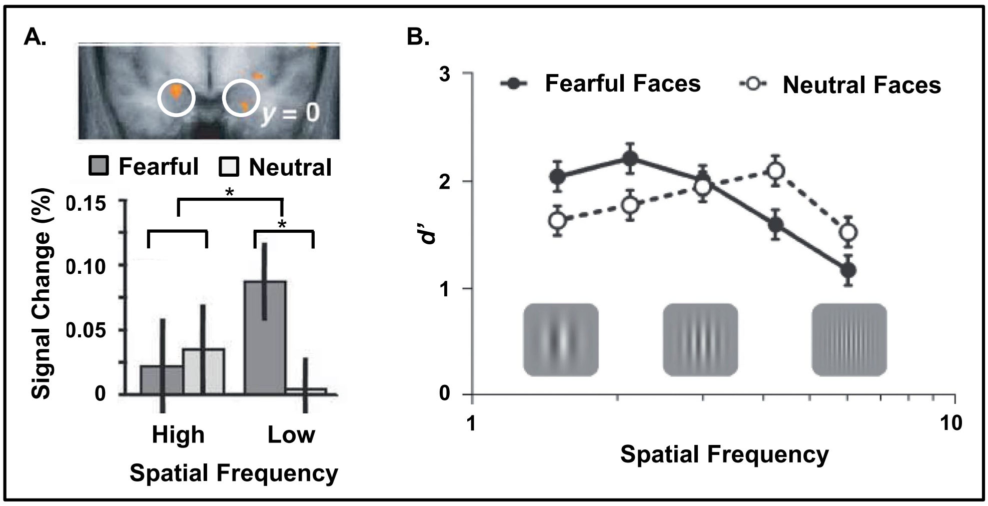


FIGURE 3
Increased amygdala sensitivity and enhanced behavioral performance linked to low spatial frequency emotional stimuli. **(A)** Amygdala shows increased sensitivity for low compared to high spatial frequency emotional information (e.g., fearful faces displayed with different frequency filters). The top view displays the bottom part of a coronal section of the brain, at the level of the amygdala (white circles). Red areas identify regions showing a significant emotional expression (fearful vs. neutral) x spatial frequency (high vs. low) interaction, evident in the bar graph. Adapted from Vuilleumier et al. (2003), with permission. **(B)** Opposing effects of emotional cues linked to spatial frequency of the targets. Fearful cues enhanced detection of low and impaired detection of high spatial frequency targets following after a short interval (40 ms). From Bocanegra and Zeelenberg (2009b), with permission.

target stimulus. The two different time windows in the AMY response modulation by emotion and attention map onto the first two time windows of target presentation, where opposing behavioral effects are identified (i.e., immediate enhancement and subsequently impaired). However, it is unclear how AMY activity relates to the later stage enhancement in target detection. One possibility is that this later enhancement is due to the release of resources that were "consumed" by the emotional relative to neutral processing. In this regard, it is also possible that, when "releasing" the emotional stimulus, the system does not gradually reset to baseline where there is a balance between bottom-up and top-down processing, but slightly oversets toward a ready-state for bottom-up processing.

Finally, an often ignored but important aspect related to such emotion-cognition interplay is the timing of neurochemical modulations associated with these phenomena, which are most evident in investigations manipulating the stress response.[2] Indeed, converging evidence from animal and human studies (reviewed in Hermans et al., 2014) points to multiple waves of neurochemical events, such as catecholamine and corticosteroid release, that influence widely distributed neuronal populations and may have opposing effects at different time scales. For instance, animal studies have demonstrated an association between prompt increases of central catecholamine levels (e.g., norepinephrine and dopamine) and enhanced scanning of the environment, following exposure to a stressor (Aston-Jones and Cohen, 2005), whereas, in humans, stress induction has been associated with enhanced detection of the second target in the attentional blink paradigm (Schwabe and Wolf, 2010). Such phenomena have been linked to a shift in locus coeruleus activity (Sara and Bouret, 2012), the main supplier of central norepinephrine, which may in turn exert opposing influences on AMY (enhancement) and the prefrontal cortex (impairment), via adrenoreceptors (Birnbaum et al., 1999; Wang et al., 2007). On the other hand, corticosteroids potentiate short-term catecholamine release under stress and also exert slow genomic effects (>1 h after stressor exposure), by altering gene transcription (Joels et al., 2012). This effect has been linked to downregulation of AMY response (Henckens et al., 2010) and enhanced response in the prefrontal cortex (PFC), coupled with improved cognitive performance (Henckens et al., 2011). Thus, future research needs to carefully dissociate between influences of emotion on cognitive processing at different time scales and better control for such temporal factors.

2.1.3 The spatial frequency of emotional information (low vs. high spatial frequency)

Another important factor in determining the impact of emotion on processing visual information is the spatial frequency of the stimuli. Simply put, spatial frequency is a measure of the density of visual information in a fixed area of space. Less dense or coarse space has low spatial frequency, whereas more dense or fine-grained space has high spatial frequency. The visual system is organized to differently accommodate these two types of visual information. Magnocellular cells and pathways are tuned to respond to low spatial frequency information, and parvocellular cells and pathways are tuned to high spatial frequency information. Investigations of amygdalar anatomy in non-human primate show that there is a predominance of magnocellular efferent projections from AMY to the visual cortices, suggesting a bias in the type of information that is enhanced (Amaral et al., 2003). Consistent with this idea, investigation of human AMY response to low vs. high spatial frequencies showed that AMY is more sensitive to low spatial frequencies (Figure 3A) (Vuilleumier et al., 2003). Therefore, it may be the case that the initial boost in perceptual processing of emotional information and/or non-emotional targets

---

[2] Literature regarding the influence of stress on cognitive processing is discussed in more detail in Section 4.

that immediately precede an emotional stimulus is found only for low spatial frequency information, while high spatial frequency information is impaired. A study examining this idea found that a fearful cue enhanced the ability to accurately identify a low spatial frequency target, but impaired accuracy for a high spatial frequency target (Figure 3B) (Bocanegra and Zeelenberg, 2009b).

When considering the function of a quick detection system to identify potential threat, from a survival perspective, it is more beneficial to first determine the presence of a potential threat, rather than the exact nature of the threat. Hence, in this sense, the "*what is it*" question matters once quick action is taken based on the initial detection, and being at a safe distance will then allow for continued processing. Indeed, the visual system is designed for a quick detection of threat with magnocellular neurons, responding faster and being linked to peripheral vision, and with parvocellular neurons, responding slower and being linked to foveal vision (Maunsell et al., 1999). As a result, a fine-grained distinction of a potential threat will only occur after fixation which is subsequent to initial detection. Along this line, and based on inherent trade-offs across these two pathways (i.e., peripheral vs. foveal concentration, fast vs. slow response, crude vs. fine-grained information), a boost in magnocellular-based visual processing should also increase temporal resolution, while a boost in parvocellular-based visual processing should impair temporal resolution. This idea was investigated using a temporal gap detection task (Bocanegra and Zeelenberg, 2011a). In this task, the low spatial frequency information in a distributed emotional cue was found to enhance the detection of a temporal gap in the presentation of a target stimulus, relative to a neutral cue. Moreover, this study also differentiated the effects of low spatial frequency emotional information on temporal vs. spatial resolution. While temporal resolution was enhanced, the low spatial frequency information of a distributed emotional cue impaired the ability to detect high spatial resolution differences in target stimuli.

Overall, the evidence reviewed in this section shows that the opposing effects of emotion on visual perception and attention have been identified in terms of dissociations between task-relevant and task-irrelevant emotional stimuli, simultaneous vs. asynchronous presentation of stimuli, and low vs. high spatial frequency information. These factors may be considered either independently or as interacting with one another, and future research should consider these factors and their possible interactions in predicting and interpreting findings regarding opposing effects of emotion on visual processing.[3]

2.2 Opposing effects of emotion on episodic memory

There is strong evidence from both animal and human research that emotional events are overall better remembered than neutral events (Dolcos and Denkova, 2008; Dolcos et al., 2012; Dolcos et al., 2006; McGaugh, 2005; Phelps, 2004). The effects of emotion on episodic memory in humans have been typically investigated using experimenter-generated stimuli, such as lists of words or sets of pictures, varying in their emotional content, which participants are encoding in laboratory settings and then their memory is tested at different intervals (e.g., from minutes to several months). Such investigations have provided strong evidence that enhanced memory for emotional stimuli is linked to amygdala's involvement and its interaction with memory-related medial temporal lobe (MTL) regions (hippocampus and the associated entorhinal, perirhinal and parahippocampal cortices). In addition, the memory-enhancing effect of emotion can also benefit from the engagement of higher order cognitive brain regions (e.g., the prefrontal and parietal cortices), through their involvement in semantic, working memory, and attentional processing (Dolcos and Denkova, 2008; Dolcos et al., 2012; Dolcos et al., 2017a).

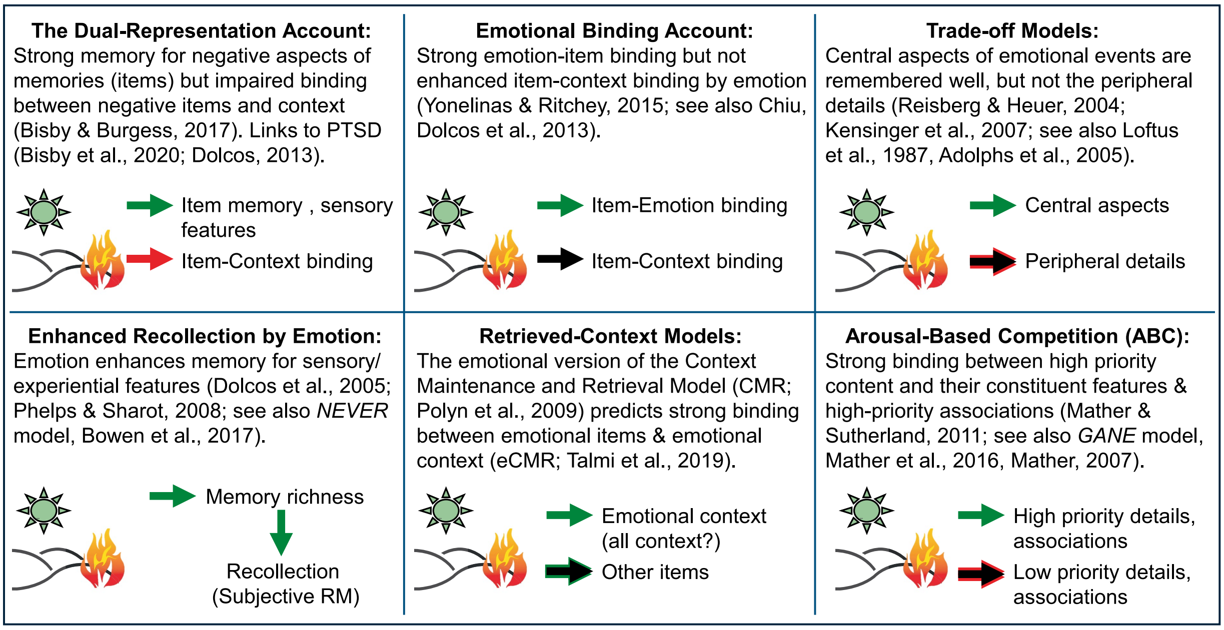
However, there is also evidence that not all aspects of an event benefit from such enhancement by emotion (Kensinger, 2009). Whereas emotion enhances memory formation for isolated or intrinsic properties of emotional items, it can also impair memory for other extrinsic aspects or memory for items in relation to other items (relational or associative memory) (Kensinger, 2009; Mather, 2007). Some evidence suggests that these opposing effects of emotion[4] are due to *central vs. peripheral trade-offs* (Kensinger, 2009), and other studies emphasize the *level of priority* (high vs. low) of emotional information in understanding enhancing vs. impairing effects of emotion on memory (Mather and Sutherland, 2011). Additionally, it has also been proposed that the opposing effects of emotion on memory might also depend on the *type of associations* (Chiu et al., 2013). Below, we discuss evidence regarding these three aspects, as well as novel evidence reconciling the opposing effects of emotion on item vs. relational memory (Bogdan et al., 2024). The latter findings also point to possible training interventions to reduce unwanted attentional biases and increase memory specificity and well-being (e.g., in affective disorders and aging).

Notably, despite various attempts, there is no unifying theory that accounts for all behavioral patterns regarding the impact of emotion on various aspect of episodic memory (see Figure 4). Although some models can account for more of the available evidence than others, no single theoretical account can explain the variety of findings. Although the amygdala has a central role in modulating emotional memories in all models, its engagement is not instrumental in the same way. For instance, a prominent view suggests that impaired relational memory

---

[3] It is important to note that this section we only discussed research investigating the effects of emotion linked to the characteristics of the stimuli, rather than to the emotional state one may be in. Indeed, one's emotional state can also impact cognition and behavior, and there is evidence that emotional state can affect visual attention and perception. Perhaps the more widely known phenomenon is the influence of mood on attentional scope, with positive mood linked to increased distributed attention and negative mood to more focused attention (Vanlessen et al., 2016; Whitmer and Gotlib, 2013). Additionally, and perhaps lesser known, is the effect of mood and emotional state on perception. Specifically, loudness, height, and distance judgements have all been shown to be influenced by one's emotional state (Anderson et al., 2011; Riener et al., 2011; Siegel and Stefanucci, 2011; Stefanucci and Proffitt, 2009; Zadra and Clore, 2011).

[4] The opposing effects of emotion on episodic memory discussed here refer to the characteristics of the information to be remembered (central vs. peripheral; prioritized vs. non-prioritized, items vs. associations), rather than to different memory stages (encoding vs. retrieval). Effects of emotion on different memory stages are discussed in detail elsewhere (Dolcos et al., 2017a; Dolcos et al., 2017b).



The Dual-Representation Account: Strong memory for negative aspects of memories (items) but impaired binding between negative items and context (Bisby & Burgess, 2017). Links to PTSD (Bisby et al., 2020; Dolcos, 2013).

Emotional Binding Account: Strong emotion-item binding but not enhanced item-context binding by emotion (Yonelinas & Ritchey, 2015; see also Chiu, Dolcos et al., 2013).

Trade-off Models: Central aspects of emotional events are remembered well, but not the peripheral details (Reisberg & Heuer, 2004; Kensinger et al., 2007; see also Loftus et al., 1987, Adolphs et al., 2005).

Enhanced Recollection by Emotion: Emotion enhances memory for sensory/experiential features (Dolcos et al., 2005; Phelps & Sharot, 2008; see also *NEVER* model, Bowen et al., 2017).

Retrieved-Context Models: The emotional version of the Context Maintenance and Retrieval Model (CMR; Polyn et al., 2009) predicts strong binding between emotional items & emotional context (eCMR; Talmi et al., 2019).

Arousal-Based Competition (ABC): Strong binding between high priority content and their constituent features & high-priority associations (Mather & Sutherland, 2011; see also *GANE* model, Mather et al., 2016, Mather, 2007).

FIGURE 4
Disagreement among models of relational memory, emphasizing the need for unifying theoretical accounts. Figure developed in collaboration with Deborah Talmi, Daniela Palombo, and Mathias Weymar for a symposium at the Cognitive Neuroscience Society Annual Meeting (Dolcos and Talmi, 2024). PTSD, Post-traumatic stress disorder; NEVER, Negative Emotional Valence Enhances Recapitulation; GANE, Glutamate Amplifies Noradrenergic Effects. The green arrows indicate enhancing effects of emotion on memory; the red arrows indicate impairing effects of emotion on memory; the black arrows indicate no effects of emotion on memory (neither enhancing not impairing).

by emotion is due to inhibitory/antagonistic effects exerted by the amygdala on hippocampal activity (Bisby and Burgess, 2017). However, challenging this view, as discussed below, we propose a new model (Bogdan et al., 2024) positing that emotion enhances relational memory through synergistic/agonistic engagement of the amygdala and hippocampus (see Figure 6). We expect that the findings by Bogdan et al. (2024) will fuel future research aimed at further clarifying the circumstances in which emotion enhances or impairs episodic relational memory.

2.2.1 The central vs. peripheral trade-off in the impact of emotion on memory

The observation that emotion enhances memory for central aspects and impairs memory for peripheral details has been initially reported in the eyewitness memory literature, which has coined the term "*weapon focus effect*." This refers to the tendency in crime witnesses to focus on the weapon and miss other details of the event (Christianson, 1992; Loftus et al., 1987). More recent research of emotional memory has referred to this phenomenon as the *central vs. peripheral trade-off* (Kensinger, 2009), the *narrowing effect of emotion on memory* (Reisberg and Heuer, 2007), or as *tunnel memory* (Safer et al., 1998). For example, Kensinger et al. (2007a) suggests a trade-off effect in memory, in which central aspects of stimuli are better remembered at the expense of remembering peripheral details (for reviews, see Kensinger, 2009; Steinmetz and Kensinger, 2013). Thus, the trade-off refers to increased memory for emotional vs. neutral items, and decreased memory for backgrounds associated with emotional vs. neutral items (see Figure 5A).

This effect is typically investigated by presenting emotionally aversive or neutral objects against neutral backgrounds (e.g., an alligator by a river, and a squirrel in a forest). Such investigations showed better memory for emotional than for neutral objects, but worse memory for neutral backgrounds when paired with emotional objects than when paired with neutral objects (Kensinger et al., 2007b; Mickley Steinmetz et al., 2012; Waring and Kensinger, 2009; Waring et al., 2010). Brain imaging studies investigating the neural correlates of these effects have shown that AMY is involved in memory-enhancing effects for aspects that are intrinsically linked to the emotional items themselves, but not for other aspects, such as the context/background in which they are encoded (Dougal et al., 2007; Kensinger et al., 2007a; Kensinger and Schacter, 2006).

2.2.2 The role of prioritization in the impact of emotion on memory

Complementary evidence suggests that opposing effects of emotion on memory are related to prioritization processes, as emphasized by the *ABC (Arousal-Biased Competition) Theory* (Mather and Sutherland, 2011). According to this theory, emotional arousal enhances encoding of high priority[5] information at the expense of low priority information (Mather and Sutherland, 2011). In a series of studies investigating the effects of emotional arousal as a function of prioritization, Mather et al. showed that emotional stimuli can enhance learning for preceding prioritized neutral objects, but impairs memory for preceding non-prioritized objects (Figure 5B) (Lee et al., 2012; Lee et al., 2014; Sakaki et al., 2014a; Sutherland and Mather,

---

[5] Of note, priority can be assigned by bottom-up salience (e.g., emotional) or by top-down (goal-relevant) relevance (Lee et al., 2012; Sakaki et al., 2014a).

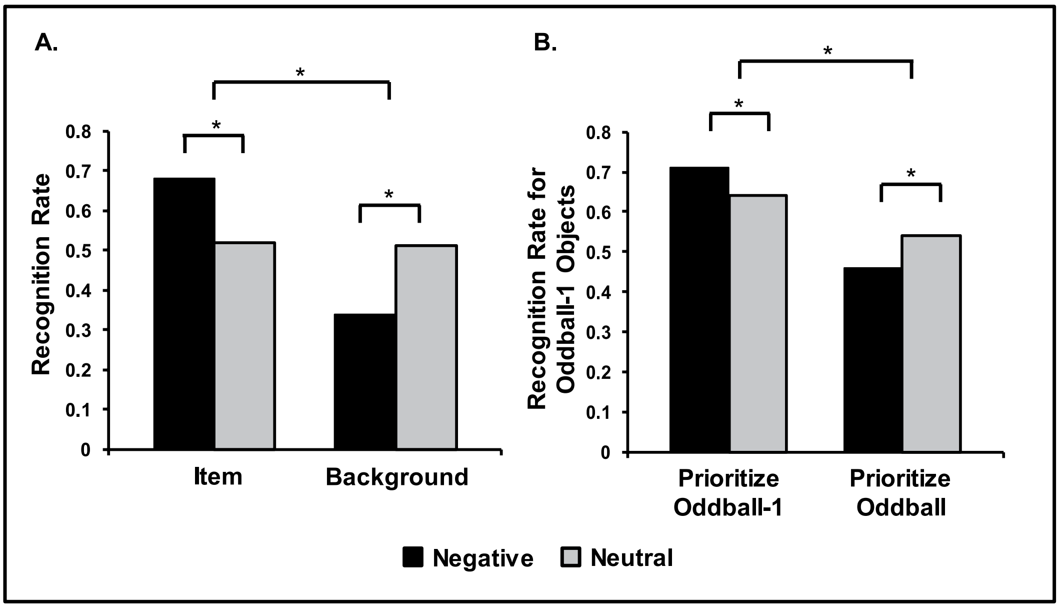


FIGURE 5
Opposing effects of emotion on episodic memory. **(A)** Central vs. Peripheral memory trade-off for items and background pictures. Negative items were remembered better than neutral items, but memory for backgrounds was lower when presented with negative items than when presented with neutral ones. Adapted from Waring et al. (2010), with permission. **(B)** Opposing effects of emotion on memory linked to prioritization. Neutral objects were better remembered when followed by negative compared to neutral oddball images, if participants prioritized the neutral objects (Prioritize Oddball-1 Condition). However, memory was worse when subjects prioritized the oddballs, instead (Prioritize Oddball Condition). Adapted from Sakaki et al. (2014a), with permission. *Significant differences.

2012). Neural evidence points to dissociable AMY involvement according to whether information is prioritized or not, as suggested by recent brain imaging studies identifying greater coupling between AMY and perceptual areas for processing high-priority stimuli (Lee et al., 2014). The ABC model can also be linked to accounts considering motivational factors to clarify the impact of emotion on memory (Levine and Edelstein, 2009; Sander et al., 2005).

2.2.3 Unitization vs. complex associations in the impact of emotion on memory

Another potential explanation for the opposite effects of emotion on episodic memory (Chiu et al., 2013) can be linked to the dissociation between memory for isolated items vs. memory for relations among items (associative or relational or memory) (Cohen and Eichenbaum, 1993; Cohen et al., 1999; Eichenbaum and Cohen, 2001). There is growing evidence from both animal and human memory research that various memory-related MTL regions can play differential roles in memory for item vs. associations (e.g., memory for an object and memory for the association between the object and its color, size, or context). Specifically, whereas the perirhinal cortex is important for encoding individual items or objects from an experience, the hippocampus (HC) is important for binding distinct item representations into memory (Brown and Aggleton, 2001; Davachi et al., 2003; Ranganath et al., 2004; Tubridy and Davachi, 2011). Further evidence also revealed that the perirhinal cortex may also contribute to some simpler forms of associative learning (Staresina and Davachi, 2010), based on unitization (Graf and Schacter, 1989). Moreover, communication between the HC and PFC plays an important part in the formation and retrieval of association-rich (episodic) memories (Moscovitch et al., 2016). Notably, the PFC regions important for association memory are also involved in emotion processing and emotion regulation (Berkers et al., 2016; Shafer and Dolcos, 2012). Therefore, the unitization of information that involves for instance assembling together different aspects of an event into a single representation via complex associations (e.g., between an object and its color) can be disrupted by emotional information, as memory supporting PFC regions can be "hijacked" by their involvement in emotion regulation operations. Importantly, in some instances, memory for isolated items and for unitized items (where different aspects of the same object are linked into a single representation) can be mediated by similar mechanisms. This is unlike the case of memory representations for more complex associations of different components of an event, as well as associations between temporally separate events, which rely heavily on hippocampal mechanisms (Ezzyat and Davachi, 2014).

Considering such possible dissociations in the available evidence, Chiu et al. (2013) has proposed that emotion enhances memory for both separate and unitized items, but it impairs memories involving more complex, HC-dependent, representations. Consistent with this idea, recent evidence points to increased engagement of the AMY and decreased engagement of the hippocampus linked to opposite effects of emotion on memory for items vs. associations, respectively (Bisby et al., 2016). These findings are also consistent with the *emotional binding model*, which posits that item-emotion binding depends on the AMY and is accompanied by slower forgetting, while item-context associations depend on the HC and are prone to more rapid forgetting (Yonelinas and Ritchey, 2015). However, the idea of differential impact of emotion on memory for unitized items vs. complex associations has yet to be tested rigorously. Also, because most of the studies have tended to focus on associations learned in laboratory settings, it remains unclear how emotion influences reactivation of previous memory representations for real-life events, in forming new associations (Sakaki et al., 2014b).

2.2.4 Reconciling opposing effects of emotion on item vs. relational memory

As mentioned above, the effects of emotion on episodic memory are not uniform. There is agreement that emotion enhances memory for individual items, but how it influences memory for the associated contextual details, or relational memory (RM), has been an issue of debate (reviewed in Bogdan et al., 2024). A prominent view suggests that emotion impairs RM (Bisby and Burgess, 2017), but there is also evidence that emotion enhances RM (Dolcos et al., 2017a). To reconcile these diverging results, a recent investigation by Bogdan et al. (2024) performed three studies incorporating the following features: (1) tested RM with increased specificity, distinguishing between subjective (recollection-based) and objective (item-context match) RM accuracy, (2) accounted for emotion-attention interactions via eye-tracking and task manipulation, and (3) used naturalistic stimuli with integrated item-context content. Challenging the view that emotion always impairs RM, this report identified both enhancing and impairing effects. Specifically, emotion enhanced subjective RM, separately and when confirmed by accurate objective RM. Emotion impaired objective RM through an attention capturing effect, but it enhanced RM accuracy when attentional effects were statistically accounted for using eye-tracking data. Third, emotion also enhanced RM when participants were cued to voluntarily focus on contextual details during encoding, likely by increasing item-context binding, as a results of disengaging from the attention-capturing emotional content. Finally, functional MRI data recorded from a subset of participants showed that emotional enhancement of RM was associated with increased activity in the medial temporal lobe (MTL) and the left ventrolateral prefrontal cortex (vlPFC), along with increased intra-MTL and vlPFC-MTL functional connectivity (Bogdan et al., 2024).

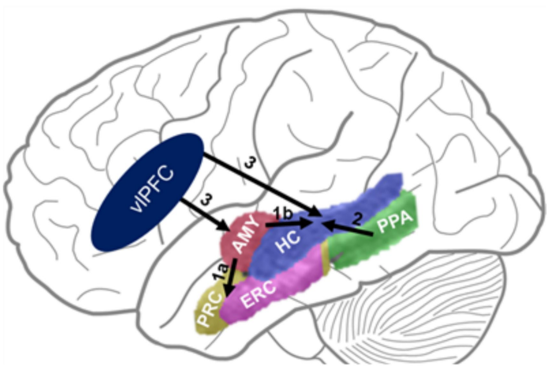


FIGURE 6
The DEAME model. Paths 1 & 2 show bottom-up influences from emotion- (AMY) and perception-related (PPA) areas on memory-related MTL regions. Path 3 shows top-down PFC influences on activity in MTL regions. Challenging the view positing agonistic (1a) vs. antagonistic (1b) influences of AMY on brain regions involved in item (PRC) vs. relational (HC) memory, respectively, we show that both paths (1a & 1b) have synergistic engagement leading to enhanced RM, together with path 2. Also, paths 1 & 2 are both susceptible to influences from the left vlPFC. AMY, Amygdala; HC, Hippocampus; PRC, Perirhinal Cortex; ERC, Entorhinal Cortex; PPA, Parahippocampal Place Area (part of the Parahippocampal Cortex Proper); PFC, vlPFC, Ventrolateral Prefrontal Cortex.

Interestingly, contrary to the view that emotion impairs memory for contextual details by inhibiting recollection-processing brain regions (HC) (Bisby and Burgess, 2017), this study found evidence of synergistic involvement of MTL regions involved in emotion (AMY) and recollection (HC) processing associated with enhanced RM by emotion. Moreover, the fMRI results point to MTL and PFC mechanisms consistent with a model of dual enhancement of associative memory by emotion (the DEAME model, Figure 6), linked to the MTL engagement orchestrated by left vlPFC influences. Specifically, maximized enhancement of subjective confirmed by objective RM when focusing on emotional aspects of stimuli was predicted by the engagement of an *emotion-to-memory* MTL route, reflected in increased activation of the AMY and HC along with functional coupling between these regions. In contrast, maximized enhancement of objective RM (item-context binding) when focusing on the contextual details of emotional stimuli was predicted by the engagement of a purported *perception-to-memory* MTL route reflected in heightened HC activation and connectivity with the PPA. Importantly, both routes are susceptible to top-down modulation from a left vlPFC area (Bogdan, et al., 2024).

These findings disrupt the status quo and have important practical applications. Affective disorders, such as depression and anxiety, along with PTSD are associated with maladaptive memory processing, resulting in memory *de*contextualization Enhanced RM by emotion through voluntary attentional focus points to possible evidence-based solutions on how these patients could grapple with unwanted emotional troubles via redirecting their attention. It is also worth noting that, outside of affective disorders, some of the strongest declines in memory, such as those associated with aging, are linked to RM. Hence, our findings also inform potential attention-based techniques that can be taught to help older adults counteract memory declines. Finally, this research also points to the role of attention in focusing on positive aspects of our experience (Denkova et al., 2015), not just away from negative ones, to increase memory and well-being.

Overall, opposing effects of emotion on episodic memory[6] have been identified in terms of dichotomies involving three main

---

[6] Similar to the case of perception and attention, one's emotional state can also impact episodic memory (Fitzgerald et al., 2011; Greene et al., 2014; Lewis et al., 2005). In short, available research suggests that emotional states can lead to differential effects depending on their congruency with the emotional information to encode and retrieve, a phenomenon known as mood-congruent memory (Blaney, 1986). For instance, memory is enhanced when the mood valence is consistent between encoding and retrieval, or when there is congruency (during encoding or retrieval) between the subject's mood and

dissociations: central vs. peripheral, high vs. low priority, and item vs. associations. Future research should consider such dissociations, to further delineate the impact of emotion on memory and the associated neural correlates, according to the type of associations, and linked to effects of emotional stimuli vs. emotional states and to modulations by previous memory representations (Sakaki et al., 2014b). This section also discussed novel evidence reconciling opposing effects of emotion on RM, which revealed fMRI findings consistent with a DEAME model of dual enhancement of associative memory by emotion in the MTL. Finally, because voluntary focus on contextual details during encoding reduces the typical attentional bias (and the associated experienced emotions; Dolcos et al., 2020a, Dolcos et al., 2020b) and enhances associative memory (Dolcos et al., 2020a; Dolcos et al., 2020b; Bogdan et al., 2024), the findings discussed here also point to possible attention-based training interventions to increase RM specificity in healthy functioning, PTSD, and aging, by promoting item-context binding and diminishing memory *de*contextualization.

It should be noted that congruent effects of emotion (e.g., enhancing) at different neurocognitive levels likely involve overlapping processes. For instance, prioritization of processing emotional information at a perceptual level leading to enhanced memory for emotional information is associated with overlapping engagement of neurochemical (noradrenergic), cognitive (attentional), and neural (amygdalar) aspects. This is similar to the link discussed in the next section, but there the overlapping mechanisms were identified linked to divergent effects of emotion across different processes (e.g., working vs. episodic memory). Interestingly, in both cases, dissociable mechanisms mediating within- and across-domains opposing effects of emotion were also identified.

3 Opposing effects of emotion across cognitive domains

Available evidence also suggests that opposite effects of emotion can be identified when linking *immediate* (impairing) and *long-term* (enhancing) effects of distracting emotional information across different domains. Specifically, there is evidence that task-irrelevant emotional distracters can impair ongoing cognitive processing (e.g., perceptual), while also leading to enhancement of memory for the distracters themselves. As discussed below, brain imaging studies have identified common and dissociable neural mechanisms for these opposing effects of emotional distraction. These studies provide neurobiological support for linking possible opposing effects of emotion in real-life situations. As alluded to earlier, task-irrelevant emotional information (passing the scene of a tragic accident while driving) may temporarily distract us from the main task (driving), while also leading to better memory for the distracting information (increased memory for the totaled cars).

3.1 Opposing effects of emotion on perception vs. episodic memory

Studies examining these effects are still scarce, but available evidence suggests that emotional distraction can, indeed, have an immediate impairing effect on perceptual processing (Shafer et al., 2012), while leading to long-term enhanced memory for the distracters themselves (Shafer and Dolcos, 2012). This study manipulated both the perceptual processing load of the main cognitive task and the emotional charge of the distracting information, and showed differential effects of the two factors on the immediate and long-term effects of emotion. Importantly, this study provided evidence that immediate/impairing and long-term/enhancing effects of emotional distraction are differentially influenced by the availability of processing resources. Specifically, the strongest immediate impairment of emotional distraction occurred when perceptual load was low, and thus more resources were available to process the distracters. However, the strongest enhancement of memory for the emotional distracters occurred when processing resources were least available (high load). Neurally, links between the two opposing effects were observed in both basic emotion processing (AMY) and higher-order processing (e.g., ventrolateral PFC; Figure 7, left panel) regions, showing overlapping effects of emotion on perception and memory. Instead, dissociations were observed mainly in higher order cognitive brain regions, showing involvement only in the immediate impairing (medial PFC) or long-term enhancing (superior parietal cortices, SPC) effects (Figure 7, right panel). Given that the medial PFC is sensitive to emotional stimuli (Keightley et al., 2003; Scheuerecker et al., 2007) and SPC is part of the attentional network (Corbetta and Shulman, 2002), their involvement in the opposing effects can be attributed to increased emotional and goal-relevant processing of the distracters, respectively.

3.2 Opposing effects of emotion on working memory vs. episodic memory

Emotional distraction can produce detrimental effects not only in tasks involving lower-level perceptual processing, but also in tasks involving higher-level processing, such as working memory (WM) (Dolcos et al., 2008; Dolcos and McCarthy, 2006; Dolcos et al., 2007). Again, studies linking immediate and long-term impact of emotion on working vs. episodic memory are scarce, but evidence from a study concomitantly investigating these opposing effects within the same participants revealed that emotional distracters presented during the delay interval between memoranda and probes in a WM task had immediate impairing effects on WM performance, while enhancing long-term memory for the distracters (Dolcos et al., 2013). This provides further evidence for the idea that emotional distracters can divert processing resources from the main WM task to processing emotional distracters (Dolcos and McCarthy, 2006), while

---

the valence of the information to be encoded/retrieved (Fitzgerald et al., 2011). The differential impact of emotional stimuli vs. emotional state is still an open question, as research trying to delineate these effects is scarce (Cohen et al., 2016). Hence, clarification of this issue is a fruitful avenue for future research, both in normal functioning and in affective disorders, which are characterized by an overall negative mood and a negative affective bias in attention, perception, and memory (Drevets, 2001).

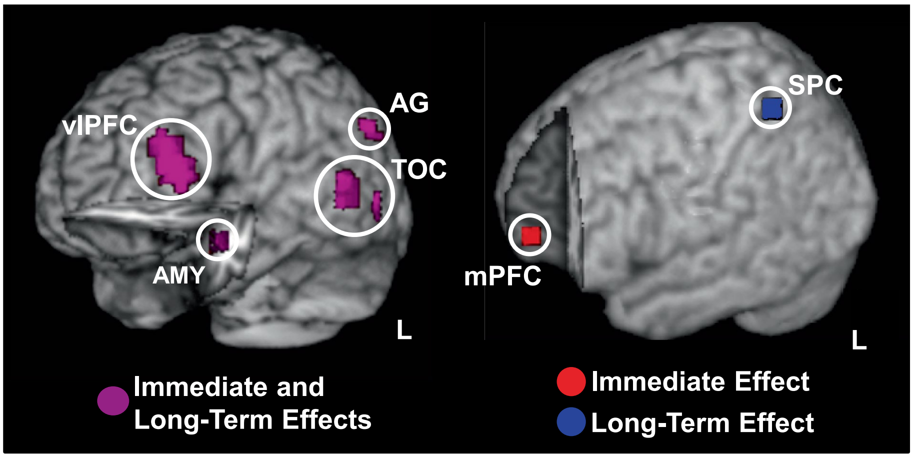


FIGURE 7
Overlaps and dissociations between brain regions involved in opposing effects of emotion on perception and episodic memory. Left panel shows overlapping responses in cortical brain regions linking the immediate/impairing effect of emotional distraction and the long-term/enhancing effect of emotional memory (shown in magenta); cut-out in the left hemisphere reveals similar responses in the AMY. Right panel shows responses dissociating between the two opposing effects of emotion, with the mPFC involved only in immediate impairment (in red) and SPC involved only in long-term enhancement (in blue). Activation maps are superimposed on high resolution brain images displayed in 3-D views using MRIcron (http://www.mccauslandcenter.sc.edu/mricro/mricron/). AG, angular gyrus; AMY, amygdala; mPFC, medial prefrontal cortex; SPC, superior parietal cortex; TOC, temporo-occipital cortex; vlPFC, ventrolateral PFC; L, Left. Adapted from Shafer and Dolcos (2012), with permission.

simultaneously initiating processing that leads to better memory for the distracters themselves (Dolcos et al., 2013).

At the brain level, trials producing both effects (impaired WM and enhanced episodic memory) were associated with decreased activity in dorsolateral PFC (linked to immediate/detrimental impact on WM performance) and increased response in MTL regions (linked to long-term/increased episodic memory performance) (Figure 8A). Of note, the same AMY region was linked to both of these opposing effects (see middle panel). Interestingly, trials associated with enhanced episodic memory performance for emotional distracters that did not disrupt WM performance were linked to increased involvement of top-down PFC mechanisms (i.e., ventrolateral PFC; Figure 8B). This suggests that enhanced memory performance for emotional distracters also benefits from the engagement of coping mechanisms engaged to deal with the presence of emotional distraction during the WM task (Dolcos et al., 2013), possibly involving deeper encoding due to more elaborative processing of the distracters (Dillon et al., 2007).

Overall, these findings demonstrate that the immediate impairing impact of emotional distraction on perception or WM and the long-term enhancing impact of emotion on episodic memory are mediated by overlapping and dissociable neural systems, involving both bottom-up and top-down mechanisms. Interestingly, the link and dissociation between the opposing effects of emotion across cognitive processes/domains could also be seen as downstream consequences of within-domain processing bias, if attention is considered the "domain" of reference. Indeed, the attention-capturing effect of emotion, leading to impaired perception/working memory by task-irrelevant emotional information, can also be responsible for enhanced episodic memory for the distracters themselves. This interpretation is complementary to the view linking the opposing effects of emotion across cognitive processes, leading to impairing immediate vs. enhanced long-term effects, as both have in common an attentional bias in processing emotional distraction.

4 Opposing effects of emotion in the stress response

4.1 Complex stress-brain interaction orchestrated by neuromodulator action

The impact of emotion on cognition can also be investigated in the context of the response to stressors.[7] Converging evidence from human and animal studies suggests that the effect of acute stress on cognition, specifically on memory, follows an inverted U-shape function, with moderate levels of stress leading to memory enhancement, and extremes levels of stress (too low or too high) leading to memory impairment (Diamond et al., 2007; Park et al., 2006; Sandi and Pinelo-Nava, 2007). Interestingly, similar effects were also observed in the hippocampal function, in the stress response (Nadel and Jacobs, 1998). Importantly, as also discussed in the next section, highly intense acute emotional events and/or chronic exposure to stressful experiences can create traumatic memories, resulting in long-lasting states of hyperarousal and in the development and persistence of affective disorders (depression, anxiety, PTSD). Indeed, while normal levels of temporary/acute stress can have adaptive function for survival, repeated and prolonged stress can be deleterious for health and survival (McEwen, 1998a, 1998b, 2007).

---

[7] Other psychophysiological states, such as being hungry or sleep deprived, may also influence cognitive processing (Benau et al., 2014; Killgore, 2010). However, due to space limitations, in this section we focus only on stress, as a representative emotional state, whose influence on cognition extends beyond the transient effects typically investigated in studies of emotion-cognition interactions (discussed in Sections 2 & 3). See also the associated footnotes from previous sections, pointing to literatures focusing on state-related effects of emotion on perception/attention and episodic memory.

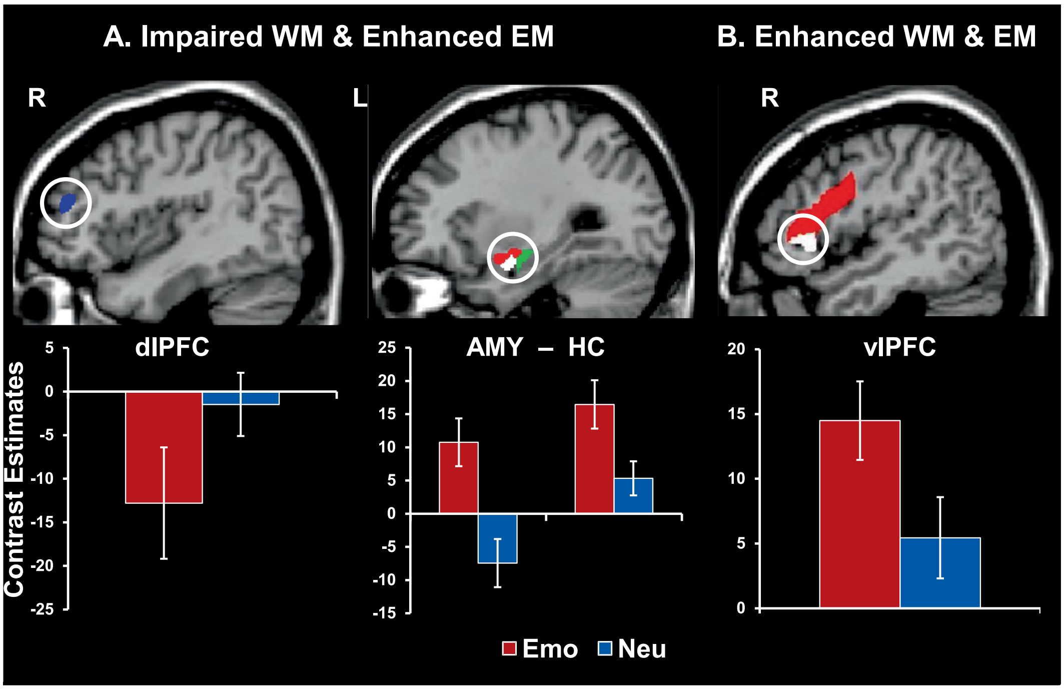


FIGURE 8
Brain activity linked to working memory (WM) impairment and/or episodic memory (EM) enhancement by emotional distraction. **(A)** Greater deactivation in the dorsolateral prefrontal cortex (dlPFC, blue area, left panel) and increased activity in both amygdala (red area) and hippocampus (green area, middle panel) were linked to impaired WM but enhanced EM performance. **(B)** Increased activity in the ventrolateral prefrontal cortex (vlPFC, red area, right panel) was also linked to enhanced WM and EM. Interestingly, subregions of the AMY and vlPFC (white areas) also had differential contribution to the impact of emotional distraction on WM, with AMY activity predicting impaired WM performance (showing a negative correlation with WM scores) and vlPFC predicting enhanced WM performance (showing a positive correlation with WM scores). The bar graphs show brain activity from peak activation voxels in the highlighted regions. The activation maps are superimposed on high-resolution brain images displayed in sagittal views. R = Right; L = Left; Emo = Emotional distraction; Neu = Neutral distraction. AMY = amygdala; HC = hippocampus. Adapted from Dolcos et al. (2013), with permission.

Acute stress can lead to *transient* hyperarousal, which promotes threat detection and memory for emotional events, through the involvement of the AMY and its connections with memory-related brain structures (McGaugh, 2000, 2004), and hence can have an adaptive outcome. By contrast, chronic stress can lead to a state of *continuous* physiological arousal and have deleterious effects on the HC (Roozendaal et al., 2009) and PFC regions (Arnsten, 2000a; Arnsten, 2009; Hains and Arnsten, 2008), hence leading to maladaptive outcomes. It is also important to note that, while historically the exposure and level of stress have been the primary topics of the majority of human and animal neuroscience stress research, recently there has also been an increased effort to understand the role of individual differences in the response to stressors (see Sections 4.2 and 4.3). The main focus here is on acute regulatory processes, as opposed to chronic stress, and the specific effects of acute stressors on cognition are also discussed linked to stress controllability and the role of individual differences (personality, genetic) in stress sensitivity.

Stressful experiences trigger activation of the hypothalamus-pituitary–adrenal (HPA) axis (Joels and Baram, 2009; Lupien et al., 2007), which affects the functioning of both emotion processing brain regions (AMY) (Roozendaal et al., 2009) and regions involved in cognitive processing (HC and PFC) (Lupien et al., 2009; Roozendaal et al., 2009). These three regions are also among the brain areas most sensitive to stress hormones, due to high density of glucocorticoid receptors, and hence not surprisingly they are also the main brain structures involved in emotional learning and memory. Stressors trigger distinct waves of spatially and temporally specific neurochemical changes that affect processing in both affective and cognitive domains (reviewed in Hermans et al., 2014). Initial exposure to stressors is first associated with increased levels of catecholamines (e.g., norepinephrine and dopamine), whose levels get back to normal shortly after stressor offset. Noradrenergic changes are widespread, affecting the whole cerebral cortex, the amygdala, thalamus, and the hypothalamus (Foote and Morrison, 1987), and may have opposite effects on neural functioning in cortical (PFC) vs. subcortical (AMY) regions (Arnsten, 1998; Arnsten, 2000b; Qin et al., 2009; van Marle et al., 2009). Dopaminergic changes occur mostly in the PFC, but also affect responses in the basal ganglia, both in ventral (nucleus accumbens) and in dorsal (caudate nucleus) striatal regions (Abercrombie et al., 1989).

In addition to the fast increases in catecholamine levels, the stress response is also associated with increases in corticosteroid levels. Corticosteroids (cortisol in humans) start to reach the brain after several minutes and when neurons are reached, they exert fast non-genomic and slower genomic effects. At a non-genomic level, corticosteroids interact with membrane-bound mineralocorticoid and glucocorticoid receptors, which are co-expressed in the hypothalamic paraventricular nucleus, AMY, and HC, but the glucocorticoid receptors are predominant in most brain regions, including the PFC (de Kloet et al., 2005). Corticosteroids also interact with catecholamines, increasing norepinephrine levels in

AMY (McReynolds et al., 2010), potentiating the effects of stress on dopamine release (Saal et al., 2003), regulating dopaminergic projections within the PFC (Butts et al., 2011), and enhancing AMY function (Roozendaal et al., 2006; Roozendaal et al., 2008). The slow genomic effects are based on transcription modulation affecting levels of multiple proteins that, in turn, affect neuronal function in multiple brain regions, over the course of hours. For instance, genomic effects modulate PFC activity and connectivity (Yuen et al., 2011) and dorsal HC activity (Karst and Joëls, 2005), a few hours after stress induction or corticosteroid application, in a way that they contribute to a normalization in the aftermath of an acute stressful event (Henckens et al., 2010, 2011; Henckens et al., 2012).

Turning to the behavioral consequence of stress responses, there is a large body of evidence from animal and human research showing that stress can have both beneficial and deleterious effects on learning and memory, reflected in enhanced encoding and consolidation of emotional events vs. impairing memory retrieval and working memory, respectively (Lupien et al., 2007; Roozendaal et al., 2009). As mentioned above, while normal levels of temporary/acute stress can have adaptive function for survival, repeated and prolonged stress can be deleterious for health and survival (McEwen, 1998a, 1998b, 2007). Opposing effects in the response to stressors can also be observed in smaller time windows. Evidence points to time-dependent manner of stress influences on brain function, affecting activity and connectivity of visual, emotional, and cognitive processing brain regions in an opposite manner, in order to overall serve adaptation to changing environmental demands. Temporal effects of cortisol on affective and cognitive functions have started being investigated relatively recently (Henckens et al., 2010, 2011; Henckens et al., 2012; Hermans et al., 2014). For instance, Henckens et al. (2012) investigated the time-dependent impact of cortisol on the neural correlates of attentional processing by using a randomized, double-blind, placebo-controlled approach, involving the following 3 groups: placebo, *fast* cortisol, and *slow* cortisol. First, results indicated that the rapid effects of corticosteroids were associated with increased bottom-up/stimulus-driven attentional processing, which caused impaired selective attention (as reflected in increased emotional interference). Neurally, these effects were associated with increased AMY activity and increased AMY-PFC connectivity while processing aversive relative to neutral distraction. These findings from the *fast* cortisol group suggest that the rapid corticosteroid effects cause stimulus-driven behavior, and can contribute, together with those of catecholamines, to a state of hypervigilance (Joels and Baram, 2009; Roozendaal et al., 2006).

Second, the slow effects of corticosteroids modulated the neural correlates of sustained attention, by reducing bottom-up processing. Specifically, the *slow* cortisol group showed reduced activation in visual brain regions linked to sustained attentional processing, as well as reduced negative connectivity between activity in the AMY and insula. These findings suggest that the slow corticosteroid effects might counteract the rapid effects by reducing automatic visual/stimulus-driven processing, and enhance the engagement of more controlled processing, to restore brain functions following stress (Dolcos, 2014). Therefore, this study proposes a more adaptive view on the impact of cortisol on attention and emotion according to the temporal profile of action, with an initial effect optimizing detection of potential threat at the cost of impaired cognitive processing, and a delayed effect normalizing cognitive brain functions following stress (Hermans et al., 2014; Joels and Baram, 2009).

Overall, extant evidence highlighting carefully orchestrated effects on executive control regions such as the PFC, and on limbic structures, such as AMY, suggests that exposure to acute stress increases activity in brain regions involved in fear and attentional vigilance, at the cost of executive control regions' function. This allocation of resources to the affective vs. executive control function reverses, as the stress subsides, normalizing the emotion-cognition balance in the aftermath of stress (Hermans et al., 2014). Notably, while these effects might allow for optimal responding to stressful situations and subsequent recovery in healthy functioning, they are likely impaired in clinical conditions such as PTSD, which is characterized by a continuous state of hypervigilance (Dolcos, 2013), as discussed in Section 5.

4.2 Presence vs. absence of controllability in the stress response

Interestingly, the effects of stress on cognition are also influenced by other factors, such as the subjective or objective *controllability*[8] of the stress. This may explain why in some circumstances and/or individuals stress impairs cognition, whereas in others it may enhance it. There is evidence that the presence of controllability can improve cognitive performance, whereas in uncontrollable situations extremely subjective experience of stress can have detrimental effects on cognitive functioning. The feeling of controllability appears to affect the functioning of the PFC, which inhibits the stress response in the AMY and hence can lead to resilient behavior (Buetti and Lleras, 2012; Henderson et al., 2012; Kerr et al., 2012). For instance, Henderson et al. (2012) investigated the effects of stress controllability and subjective perception of stress on performance on a color-word Stroop task separated by a stress induction block, which was controllable for some participants and uncontrollable for others. Interestingly, controllable stress that was experienced as moderately intense was linked to improved performance (reduced interference), whereas uncontrollable or extreme stress impaired performance (Figure 9). Similarly, even just the subjective feeling of control seems to affect performance (Buetti and Lleras, 2012; Mereu and Lleras, 2013). Buetti and Lleras (2012) investigated the effects of the feeling of control on time perception (estimated duration) of emotional events, and showed that in situations of feeling of control emotion does not impact time perception, whereas in the absence or low feeling of control, time perception is impacted by emotion – that is, negative events are perceived as longer-lasting than positive events, regardless of their level of arousal.

At the neural level, the presence of stress controllability has been associated with the involvement of the ventromedial PFC (vmPFC) (Kerr et al., 2012). Investigation of the effects of stress controllability on the neural correlates of anticipatory response to aversive stimuli in snake-phobic participants showed that controllable anticipatory responses were associated with increased vmPFC activity (Kerr et al., 2012). This finding provides evidence for its involvement in reducing stress responses when stress is controllable, likely by inhibiting AMY responses and promoting resilient behavior. On the other hand,

---

[8] Although some definitions of stress imply uncontrollability, here we refer to studies specifically manipulating controllability.

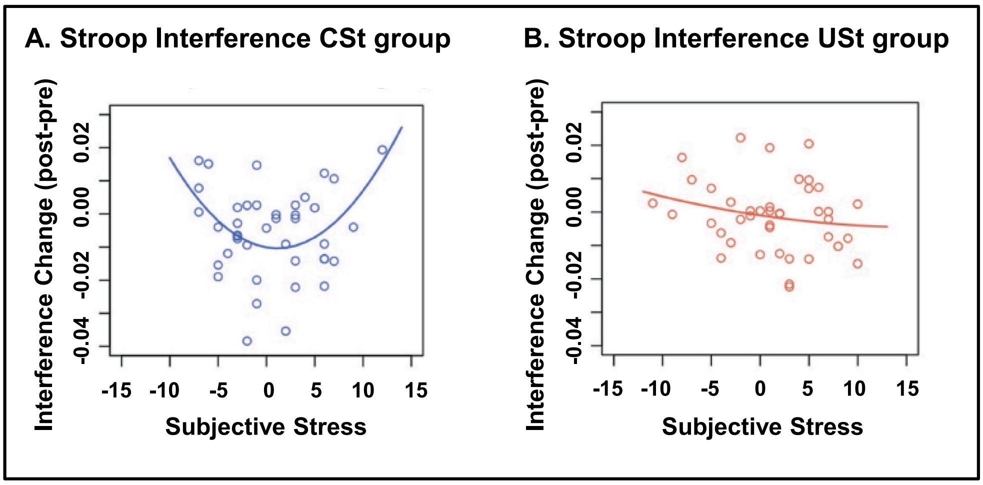


FIGURE 9
Stroop interference as a function of controllability and subjective stress. **(A)** In the group with controllable stress (CSt), moderate levels of subjective stress were associated with improved Stroop performance (reduced interference), whereas low or high levels of subjective stress were related to impaired Stroop performance (left panel). **(B)** In the group with uncontrollable stress (USt), subjective stress was not related to Stroop performance (right panel). From Henderson et al. (2012), with permission.

decreased activity in vmPFC has been observed during repeated stressful tasks in subjects who had experienced early-life stress (Wang et al., 2013), which could also be linked to stress uncontrollability in those participants. Specifically, during a repeated stressful task, subjects who had experienced early-life stress, and were also high in trait rumination, had reduced vmPFC activity in the later compared to earlier stressful trials. However, subjects who had experienced early-life stress, but were high in trait mindfulness showed sustained vmPFC activity, and subjects without history of early-life stress had an increased vmPFC response over time. Together, these findings suggest that the presence of control (or the feeling thereof) during stressful situations engages PFC mechanisms that regulate emotional reactions in AMY, and the engagement of these mechanism is affected by previous stress history and personality traits.

4.3 The role of individual differences in the stress response

Although research showed that stress can have important consequences on cognition and behavior, and hence can impact physical and psychological well-being, it is also known that stress is not experienced the same way by different individuals (Johnstone and Feeney, 2015). Here, we briefly discuss personality-related differences and then highlight evidence regarding genetic differences in the stress response. Regarding personality differences, neuroticism has been probably the most studied trait regarding individual differences in the response to stressful situations (Canli, 2004; Everaerd et al., 2015; Gunthert et al., 1999), and there is also evidence that high neuroticism is also linked to clinical conditions, such as anxiety and depression (Ormel et al., 2013). As discussed above, there is evidence pointing to individual differences in personality traits indexing coping mechanisms (Wang et al., 2013), and their link with brain functioning associated with early-life stress exposure. The differential vmPFC activity in individuals who experienced early-life stress and were high in trait rumination *vs.* high in trait mindfulness, highlight the response of this region as an important neuroimaging marker distinguishing stress vulnerability vs. resilience in individuals with early-life stress. In addition, early-life stress exposure can also interact with individual differences linked to traits reflecting habitual use of emotion regulation strategies, such as reappraisal, which has been linked to better mood and more adaptive stress responses (Khawli et al., 2017).

Hence, consideration of individual variations would help better understand why in the same circumstances, some people may be more susceptible to stress effects and even develop affective disorders, while others are more resistant against aversive effects of stress. Related to this, an important emerging area of research (McEwen, 2016) targets ways of building resilience, particularly in the case of high-demand, high-risk occupations, such as Army service members and first responders (de Terte and Stephens, 2014). Consistent with the evidence mentioned above, one such successful way of achieving this has been through mindfulness training (Jha et al., 2010). Indeed, mindfulness training in soldiers has been associated with benefits to both cognitive and affective functioning (Jha et al., 2015; Jha et al., 2010). Moreover, increased mindfulness has also been linked to increased resilience and less burnout in first responders (Kaplan et al., 2017). Other training programs targeting emotion control strategies have also proven successful in increasing resilience and well-being (Dolcos et al., 2021).

In addition to individual variations linked to personality, subjective perception, or previous history of stress, genetic variations can also modulate the effects of stress. Evidence suggests that the opposing effects of stress on memory could be linked to variations in the gene encoding Catechol-O-methyltransferase (COMT), which are linked to individual differences in basal catecholaminergic availability (Qin et al., 2012). For instance, Qin et al. (2012) investigated how COMT genotype (COMT Met homozygotes vs. Val carriers) modulates the effects of moderate stress on WM performance and the associated neural correlates. Behavioral and fMRI data were recorded while participants performed an N-back WM task preceded and followed by either stressful or neutral movies. The results revealed COMT genotype-dependent effects of stress on WM performance and on WM-related activations, in the PFC, and deactivations in the MTL. Specifically, moderate stress led to negative impact in COMT Met homozygotes (characterized by higher baseline catecholaminergic activity), and positive impact in Val carriers (Figure 10).

These effects appear to depend on the baseline catecholaminergic activity, and to follow an inverted-U curve. Val carriers start with a lower (sub-optimal) baseline level of catecholaminergic activity and under moderate stress this activity increases to optimal levels so that it leads to optimal performance and increased dorsolateral PFC activation together with stronger deactivation of the MTL, extending to the AMY. The opposite pattern is observed in Met homozygotes, which start already with higher baseline levels of catecholamines, and moderate stress induction leads therefore to their stronger elevation resulting in impaired performance and decreased PFC activation together with less deactivation in the MTL. Overall, these findings suggest that COMT Met-homozygotes are more susceptible to detrimental effects of stress, whereas Val-carriers are more resilient.

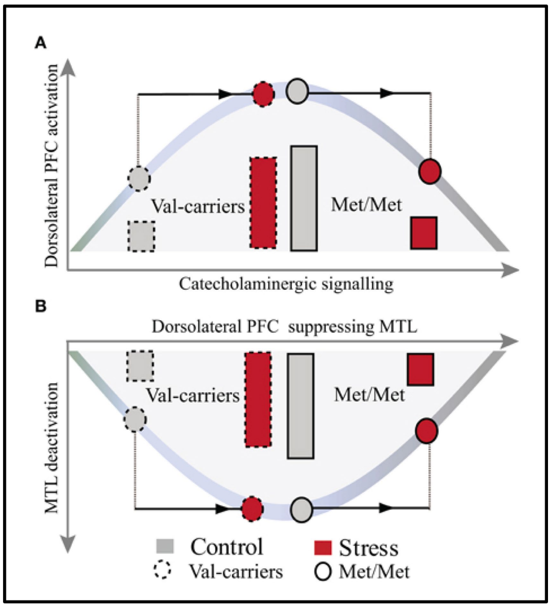


FIGURE 10
Model illustrating the effects of COMT genotype and moderate stress on WM-Related activations in dorsolateral PFC **(A)** and Deactivations in MTL **(B)**. The model reveals opposite patterns in the effects of moderate stress on dorsolateral PFC activation and MTL deactivation, in Val carriers and Met homozygotes (Met/Met), linked to the basal level of catecholamines. In Val carriers, characterized by suboptimal baseline catecholaminergic activity (see left side of the curve in A, grey-dashed line pattern), moderate stress has positive effects by increasing catecholaminergic activity (top of the curve in A, red-dashed line pattern). This leads to optimal activity in PFC and stronger deactivation in MTL (bottom of the curve in B, red-dashed line patterns). By contrast, in Met homozygotes, characterized by already higher level baseline catecholaminergic activity (top of the curve in A, grey-full line pattern), moderate stress leads to even stronger elevation of catecholamines (right side of the curve in A, red-full line pattern). This results in altered functioning of PFC and less deactivation in MTL (right side of the curve in B, red-full line pattern). PFC, prefrontal cortex; MTL, medial temporal lobe. From Qin et al. (2012), with permission.

Collectively, evidence regarding the impact of stress on cognition suggests opposite effects linked to the level of stress, the presence or absence of controllability, and linked to individual differences in personality traits and genes. Namely, optimal and controllable levels of stress can have beneficial effects on cognition and behavior, whereas extreme and repeated stress impairs cognition and may lead to the development of affective disturbances. Neurally, the available evidence suggests that the actual/objective presence, or just the mere subjective feeling, of control over stressful situations engages PFC mechanisms that regulate emotional reactions in the AMY. Moreover, PFC functioning in response to stressors has been also linked to individual variations in personality traits indexing vulnerability to (trait rumination) or resistance against (train mindfulness) emotional dysregulation, as well as to genetic differences associated with susceptibility to (COMT Met-homozygotes) or resilience against (Val-carriers) stress. This sections also points to training interventions to increase resilience and well-being (Dolcos et al., 2021; Jha et al., 2010).

5 Linking opposing effects of emotion on cognition in affective dysfunctions: the case of PTSD

In vulnerable individuals, stressful life events may cause PTSD, which is associated with highly intense and intrusive memories and thoughts that disrupt normal daily functioning. This clinical condition is characterized by changes in both emotional and cognitive processing, typically reflected in increased emotional reactivity (*hypervigilance* toward potential threats in the environment) and uncontrollable recollection of traumatic memories, which reflect impaired cognitive/executive control (Brown and Morey, 2012; Hayes et al., 2012; Rauch et al., 2006; Shin and Liberzon, 2009). These changes are reflected in regions associated with functions that may be enhanced (AMY) or impaired (PFC) by emotion. Findings from a fMRI study of emotional memory showed reduced activity in the AMY-MTL memory system, during memory encoding, suggesting dysfunction of the mechanisms typically involved in emotional memory. Interestingly, this altered brain activity during encoding was accompanied by increased false alarm rates during retrieval, in PTSD participants compared to a trauma exposed control participants (Hayes et al., 2011). This is consistent with non-specific (gist-based) memory for trauma-related material in PTSD, likely due to dysfunctional engagement of the MTL mechanisms during encoding, due to hyperarousal (Figure 11A). In addition, findings from a fMRI study of WM with emotional distraction showed that the PTSD group also had greater trauma-specific activation than the control group in main emotion processing brain regions, including the AMY and vlPFC, as well as in perceptual brain regions susceptible to emotion modulation (e.g., fusiform gyrus) (Morey et al., 2009). Importantly, though, the PTSD group also showed greater non-specific disruption of activity to both combat-related and neutral task-irrelevant distracters in brain regions that subserve the ability to maintain focus on goal-relevant information, including the dlPFC (Figure 11B). This undifferentiated dlPFC response to combat and non-combat distracters in PTSD is consistent with the *hypervigilance* hypothesis that may explain enhanced response to, and distracting effect of, neutral stimuli.

This evidence suggests a link between the initial impact of emotion influencing episodic memory and the impact of their retrieval triggered

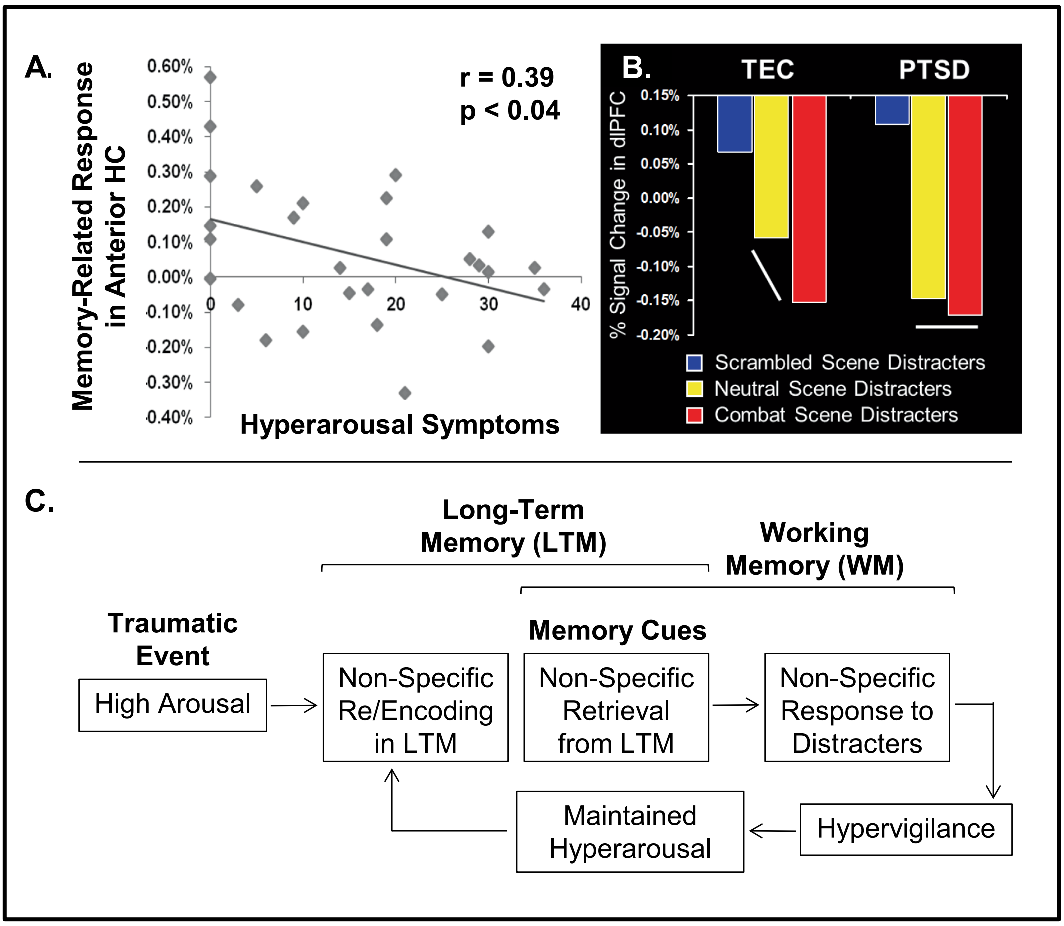


FIGURE 11
Changes in MTL and prefrontal regions activity pointing to a possible link between enhancing and impairing effects of emotion, in PTSD. **(A)** Reduced memory-related activity for trauma-related pictures in the anterior hippocampus (HC) linked to increased symptoms of arousal suggests impaired encoding of traumatic memories. Adapted from Hayes et al. (2011), with permission. **(B)** Comparison of brain activity in dlPFC during the active maintenance period of a working memory task in the PTSD and Trauma-Exposed Control (TEC) groups points to non-specific disruption of dlPFC response to salient task-irrelevant distracter scenes in the PTSD group, which unlike the TEC groups showed an undifferentiated response in the dlPFC to combat and neutral distracters. dlPFC = dorsolateral prefrontal cortex. Adapted from Morey et al. (2009), with permission. **(C)** Diagram illustrating a possible link between the impact of emotion on long-term memory and working memory in PTSD, which could be initiated and maintained due to non-specific effects of heightened arousal. From Dolcos (2013), with permission.

by trauma-related pictures presented as task-irrelevant distracters during the WM task (Figure 11C). Specifically, reduced AMY-HC engagement during the formation of memory for trauma-related pictures in the episodic memory study may be explained by initial non-specific encoding of gist-based, decontextualized representations, instead of specific and detailed contextual details of the trauma-related memories, due to hyperarousal. This, in turn, leads to non-specific responses in dlPFC, when trauma-related and neutral stimuli (external or internal; Dolcos and McCarthy, 2006; Iordan et al., 2019) are presented as task-irrelevant distracters, and to symptoms of *hypervigilance*, which contribute to the maintenance of a *hyperarousal* state and to non-specific (re)encoding of traumatic memories, in a continuous vicious cycle (Dolcos, 2013). This view is consistent with possible interpretation of PTSD symptoms (e.g., enhanced threat detection, disrupted executive control) as context dependent outcomes linked to a common cause — i.e., over-prioritization of threat-related external stimuli and internal trauma-related thoughts that can disrupt cognitive processing (e.g., Hirsch and Mathews, 2012).

In summary, this evidence points to general and specific emotional and cognitive disturbances in PTSD, which are linked to alterations in the neural circuitry underlying emotion-cognition interactions, and impact both immediate and long-term effects of emotion on working and episodic memory, respectively.

6 Comparing opposing effects of emotion on cognition across fields: healthy aging vs. depression

Evidence for opposing influences on emotion can also be identified in comparisons across groups with opposing emotional biases, such as healthy aging (showing a positive affective bias) vs. depression (showing a negative affective bias). Direct comparisons of the neural mechanisms underlying such opposing affective biases could help determine whether the biases observed behaviorally are also reflected in the neural responses associated with differences in the ability to control emotions observed in these two groups (i.e., impaired in depression vs. enhanced in healthy aging). Aging is associated not only with well-known co-morbidities and losses but also with relatively high levels of emotional well-being, possibly as a result of a *positive affective bias* in processing emotional information (Mather, 2012; Mather and Carstensen, 2005). The idea of a positivity bias in aging is supported by evidence showing that older adults tend to (i) pay attention to and remember more positive information (Charles et al., 2003; Isaacowitz et al., 2006; Mather and Carstensen, 2003) and (ii) show reduced processing of negative information, compared to young adults (Grühn et al., 2007; Wood and Kisley, 2006). From a clinical perspective, older adults have lower rates of depression and anxiety disorders compared with younger adults, indicating cohort differences that may reflect an aging-related decrease in negative affect (Jorm, 2000; Kryla-Lighthall and Mather, 2009). However, older adults' ability to shield their thoughts and emotions from negative situations suggests an enhanced ability to control emotions (Dolcos et al., 2014; Gross et al., 1997). Notably, similar to the contrast discussed in the case of PTSD, the opposing affective biases observed in healthy aging vs. depression could also be seen as potentially reflecting context dependent outcomes linked to a common process — i.e., opposing valence-dependent prioritization in processing affective information.

Neuroimaging evidence confirms the emotion-regulation account for the positivity bias (for a review, see Nashiro et al., 2012), and points to the role of the medial PFC (mPFC) and the adjacent anterior cingulate cortex (ACC) in the regulation of negative and positive emotions (Dolcos et al., 2014; Gutchess et al., 2007; Kensinger and Schacter, 2008; Leclerc and Kensinger, 2008; St Jacques et al., 2010; Tessitore et al., 2005). Moreover, there is also evidence of increased functional connectivity between the ACC and AMY in healthy older adults, who also showed overall reduced emotional ratings in response to viewing negative pictures (St Jacques et al., 2010) (Figure 12A).

Interestingly, the age differences in the ACC-AMY interactions were associated with changes in the perceived emotional content of negative pictures, reflected in more "neutral" ratings given by the older participants to the negative pictures (St Jacques et al., 2010). This suggests a role of this region in down-regulating the response to negative stimuli, possibly by reducing AMY activity when regulation is successful. This idea was recently confirmed by evidence that activity in similar ACC areas was negatively correlated with the behavioral ratings for negative stimuli in older adults (Dolcos et al., 2014) (Figure 12B), thus providing further support for a role of this region in spontaneous down-regulation of negative emotions in healthy aging.

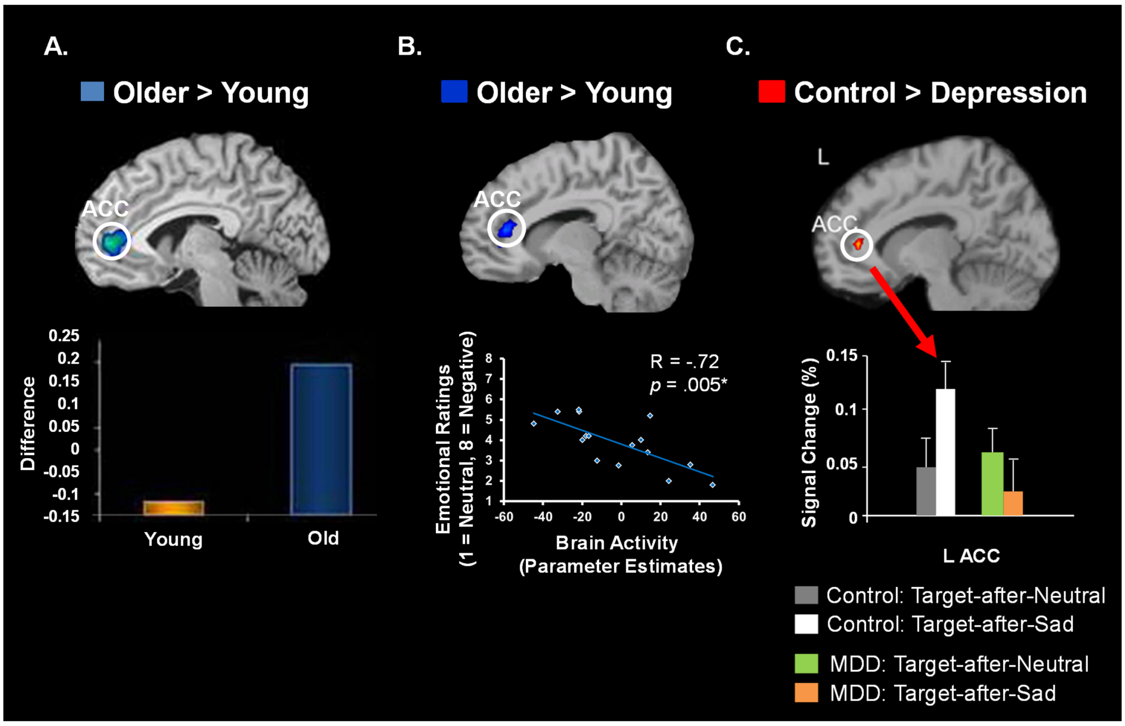


FIGURE 12
Converging evidence from healthy aging and depression regarding the role of ACC in emotion regulation. Comparison of findings from populations showing contrasting affective biases in the domain of emotion regulation point to similar neural circuitry linked to enhanced (healthy aging; A & B) vs. diminished (depression; **C**) cognitive control of emotion. **(A)** Increased functional connectivity between the amygdala and the anterior cingulate cortex (ACC) in the healthy aging group, who also showed reduced emotional ratings in response to viewing negative pictures. The y-axis represents the difference in trial-level correlations between negative and neutral conditions; adapted from St Jacques et al. (2010), with permission. **(B)** Increased activity in ACC linked to reduced ratings for negative pictures in healthy older adults, consistent with habitual engagement of emotion regulation strategies in this group; adapted from Dolcos et al. (2014), with permission. **(C)** Decreased ACC activity in patients diagnosed with major depressive disorder (MDD), who also showed impaired ability to disengage from processing mood-congruent sad distracters; adapted from Wang et al. (2008), with permission.

Interestingly, available evidence links similar brain regions to diminished ability to disengage from processing task-irrelevant negative emotional information in depression (Wang et al., 2008), which is associated with in a negative *affective bias* in processing emotional information (Gotlib et al., 2005; Koster et al., 2005; Siegle et al., 2002). Clinical studies have linked impaired executive control and enhanced emotional distractibility observed in depression to dysfunctional interactions between neural systems involved in cognitive/executive and emotion processing (Drevets, 2001; Mayberg, 1997; Mayberg et al., 1999). Studies using fMRI in depressed patients have reported activity changes in the medial frontal regions (Price and Drevets, 2009), particularly the ACC, as well as in the AMY and other limbic structures (see review by Drevets, 2001). Several studies have also described transient exaggerated activity in ventral frontal and limbic regions, including the AMY (Fu et al., 2004; Sheline et al., 2001; Siegle et al., 2002), in young adults with depression during processing of negative emotional stimuli, although this enhanced activity is not always found (Davidson et al., 2003). Similarly, transient increases or decreases in the dlPFC activity have been reported in depressed patients while performing cognitive tasks (Harvey et al., 2005; Matsuo et al., 2007; Siegle et al., 2007; Wagner et al., 2006). Interestingly, consistent with reduced emotion control in depression, recent evidence (Wang et al., 2008) points to dysfunctional ACC responses following emotional distraction, in areas overlapping with those identified in healthy aging as showing increased response linked to enhanced ability to control emotions (Figure 12C).

The role of these medial frontal regions in the depressive symptomatology is further emphasized by the results of therapeutic interventions showing normalizations of mPFC and AMY activity following pharmacological and non-pharmacological treatments. For instance, pharmacological antidepressant treatments typically report normalization of pre-treatment activity differences in mPFC (Fitzgerald et al., 2008; Mayberg et al., 1999) and AMY (Anand et al., 2007; Sheline et al., 2001). Notably, similar effects in restoring brain function have also been obtained using non-drug therapy, such as cognitive behavioral therapy. Namely, there is evidence of normalized mPFC and AMY activity, following cognitive behavioral therapy, and of a link between increased mPFC activity at baseline and treatment-related improvements (Ritchey et al., 2011). Again, the medial frontal area sensitive to these effects is located in close vicinity to the ACC areas linked to dissociable ability to control emotion in healthy aging (enhanced) vs. depression (impaired) illustrated in Figure 12. Consistent with mPFC/ACC activity as a possible neural marker of treatment-related improvement, there is also evidence of normalized resting-state functional connectivity between mPFC and AMY, consistent with reduced bottom-up influences from emotion processing regions, following emotion control training (Dolcos et al., 2021).

Together, this evidence from groups with opposing emotional biases identify activity in the mPFC/ACC as a biological marker of emotional resilience vs. vulnerability in healthy aging vs. depression, respectively, hence linking its response to differential ability to control emotional responses in these groups. Importantly, therapeutic interventions improve emotion regulation processes in depressed patients by normalizing activity in these areas. Therefore, direct comparisons of these groups with opposing emotional biases and emotion regulation abilities provide an exciting research avenue in addressing mental health issues associated by emotional dysregulation. Such studies can lead to identification of additional neural markers that can be targeted in therapeutic interventions.

7 Conclusions and future directions

The overarching goal of the present review was to discuss emerging findings from studies identifying enhancing and impairing effects of emotion on cognition at different levels of analysis. Available research provides evidence that these opposing effects of emotions can be observed within *the same cognitive domains*, *across cognitive domains*, at the more general level of the *response to stressors*, as well as *within clinical groups* and *across groups* with opposing affective biases. Importantly, these multilevel[9] relations are also influenced by individual differences, which underlines the need for adopting a comprehensive view in studies examining emotion-cognition interactions, in both healthy and clinical populations. The main conclusions of the present review are summarized below and followed by open questions for future research.

Investigation of the opposing effects of emotion within the *same cognitive domains* focused mainly on enhancing and impairing influences on perceptual/attentional and episodic memory processes. Findings concerning the impact of emotion on visual perception and attention point to the critical role of intrinsic factors, such as prioritization of emotional information processing and differential susceptibility to modulation by attention along the time-course of the emotional response, in eliciting enhancing and impairing effects. In addition, task-related contingencies, such as the context of the emotional information (task-relevant vs. irrelevant) and its presentation timing relative to non-emotional information (simultaneous vs. asynchronous), also play a substantial role in these effects. Neurally, these opposing behavioral effects are predominantly linked to the involvement of the AMY, which is sensitive to initial bottom-up prioritization and influences allocation of cortical resources to process emotional information. Similarly, the opposing effects of emotion on episodic memory have been linked to

---

[9] As discussed, emotional information can enhance or impair cognition depending on various factors, including its relevance to the present goals. For instance, emotion can help perception and memory, when task-relevant, or it can be distracting, when task-irrelevant. In this context, although not the focus of the current review, it is worth mentioning that emotional information also influences the behavioral consequences of affective processing, reflected in motor control/action. Interestingly, recent evidence shows that the valence of emotional facial (Mancini et al., 2022; Mirabella et al., 2023; Montalti and Mirabella, 2023) and body postures (Calbi et al., 2022) expressions elicit a consistent behavioral effect only when they are goal-relevant, regardless of the effectors used to provide responses (e.g., hand, arm, legs) or the type of required responses (i.e., moving or refraining from moving). In contrast, when the stimuli' emotional content is task-irrelevant, it does not affect motor control; see also Mirabella et al. (2024), for evidence regarding the neural correlates associated with the task-relevant effects mentioned above. Overall, this evidence adds nuance to the present discussion regarding opposing effect of emotion of various aspects of cognitive processing and further points to the importance of also considering the behavioral consequences of emotion processing.

dissociable engagement of the AMY according to the differential impact of arousal on various aspects of the information to be remembered (e.g., central vs. peripheral, high- vs. low-prioritized). More generic dissociations between singular or unitized items' encoding and formation of complex associations, also contribute to the opposing effects of emotion on different aspects of episodic memory. In this more comprehensive perspective, emotion may lead to memory enhancement of separate as well as unitized items, but to impairment of more complex HC-dependent memory representations. However, novel evidence provides reconciling evidence regarding the impact of emotion on RM, which highlights the importance of considering different aspects of emotional events and their complex interactions that lead to successful memory formation and retrieval.

Evidence from studies investigating impairing and enhancing effects of emotion *across cognitive domains*, such as perception and WM vs. episodic memory, points to both overlapping and dissociating mechanisms involved in the two opposing effects. Bottom-up AMY-MTL mechanisms are involved in both the impairing and enhancing effects of emotion on perception/WM vs. episodic memory. Top-down PFC mechanisms dissociate between the enhancing and impairing effects, pointing to a dorsal-ventral distinction between PFC mechanisms involved in maintenance of goal-relevant information (dlPFC), and the ones involved in coping with emotional distraction linked to enhanced episodic memory for the distracters themselves (vlPFC).

The opposing effects of *acute stress* on cognition have been linked to a variety of factors, ranging from the objective properties of the stressors and the subjective experience of stress to individual variations in personality traits and genotype, reflected in a differential engagement and interplay between MTL and PFC mechanisms. Available evidence points to carefully orchestrated neuromodulatory effects on executive control regions such as the PFC, and the limbic and subcortical structures such as the AMY, involved in emotional and attentional vigilance. Initial involvement of the latter comes at the cost of the engagement of the former, but as the stress subsides allocation of resources to the affective and executive control function reverses, hence normalizing the emotion-cognition balance in the aftermath of stress.

The opposing effects of emotion tend to co-occur and are both deleterious in affective disorders, such as PTSD, where uncontrolled recollection of distressing memories leading to impaired cognition due to emotional distraction could be linked to non-specific effects of heightened initial and perpetuated arousal. These effects also point to alterations of both bottom-up and top-down mechanisms in affective disorders. Finally, evidence from *across-fields comparisons* of groups with opposing emotional biases, such as healthy aging (showing a positive bias) vs. depression (showing a negative bias), identified the mPFC/ACC as biological markers of emotional resilience/vulnerability. This evidence links enhanced response in this region with increased ability to control emotions, characterizing healthy aging, and decreased response with impaired emotion control characterizing depression. Findings from these groups with opposing emotional biases highlight the benefits of across-group comparisons and suggest that capitalizing on the "elders' wisdom" in emotion control is a viable strategy in addressing mental health issues.

Despite significant progress in clarifying the mechanisms underlying opposing effects of emotion, important open questions still remain. In the reminder of this section, we will elaborate on some of the most prominent emerging topics that need to be considered in future investigations.

1 Future research on the enhancing and impairing effects of emotion on visual perception and attention could examine how *inter-* and *intra*-individual differences, and/or availability of attentional resource at the time of emotion processing, influence the magnitude of these effects. For example, it would be informative to determine if the relation between individual differences and the degree of emotion's impact is dependent upon the specific effect examined (i.e., enhancing vs. impairing). There is evidence that enhancing effects (better memory for emotional events) are more stable and systematically observed across individuals, whereas impairing effects (increased emotional distraction) are more susceptible to individual variations (Dolcos et al., 2013). However, it is not known whether individual differences in emotional or cognitive domain (or their interaction) are more predictive of impairing effects, and maybe differentially suited for modulating the link between opposing effects of emotion, linked to various cognitive aspects. That is, it is possible that inter-individual differences in the emotional domain may more optimally explain opposing effects of emotion linked to the attention-insensitive time window of the emotion response, whereas inter-individual differences in the cognitive domain may better explain opposing effects related to time window(s) that are more attention sensitive. Aside from clarifying inter-individual differences, it is also relevant to examine the role of intra-individual/state differences, such as linked to menstrual cycle (Sacher et al., 2013), sleep deprivation (Krause et al., 2017), different developmental stages (Ladouceur, 2012), or recent (traumatic) experiences (Hayes et al., 2012), in the interplay between emotion and cognition. Finally, while the influence of the attentional resources on the impact of emotion on lower level perceptual processes has been clarified (Shafer et al., 2012), it is less clear how manipulation of attentional resources within higher level cognitive processes can modulate the impact of emotion (but see Clarke and Johnstone, 2013) and how they are modulated by intra- and inter-individual differences.

2 Regarding episodic memory, an important issue concerns the opposing effects of emotion on associative or relational memory. The idea of differential impact of emotion on memory for items vs. their associated context has only recently been tested more rigorously (Bogdan et al., 2024). By accounting for attention effects (both with eye-tracking and through task manipulation) and also measuring memory for associations more completely (both subjectively and objectively), Bogdan et al. (2024) demonstrated the circumstances in which emotion impairs or enhances RM. Notably, the latter evidence points to ways in which forgetting the contextual details of intense emotional circumstances or stressful events can be prevented. These findings not only disrupt the status quo at the theoretical level, but also has practical implications about what we can do to control, channel, and capitalize on the emotions' energy to remember better. Moreover, this study also identified the involvement of specific MTL and vlPFC mechanisms, whose

engagement and interaction result in enhanced RM by emotion. The findings reported by Bogdan et al. (2024) are consistent with a model of dual enhancement of associative memory by emotion (DEAME) in the MTL, but more research is needed to identify the contribution of the two MTL routes mentioned above (*emotion-to-memory* and *perception-to-memory*). Other aspects that deserve further attention are related to the clarification of the emotion's effects on memory for other associations, such as those assessed by tests of source memory (see Ventura-Bort et al., 2024, in the present Research Topic), as well as those involving temporal associations (Bogdan et al., 2023a; Talmi and Palombo, 2024) and spatio-temporal integration.

3 Further insights regarding opposing effects of emotion within and across processes could be provided by linking the interplay between enhancing and impairing effects of emotion with interactions between the main functional networks of the brain. Converging evidence from investigations of *large-scale brain organization* and from affective neuroscience suggests that emotion-cognition interactions elicit specific patterns of response in brain regions associated with the major brain networks. Current models of brain organization (e.g., Bressler and Menon, 2010; Seeley et al., 2007; Yeo et al., 2011) typically describe several major functional networks, such as the central-executive, salience, and default-mode networks, which implement domain-general functions, such as executive control, orienting toward motivationally salient stimuli, and self-referential processing, respectively (for alternative but compatible conceptualizations, see Dosenbach et al., 2006; Dosenbach et al., 2008; Dosenbach et al., 2007; Gordon et al., 2014; Power et al., 2011; Power and Petersen, 2013). Although subtle separations between these networks are still a matter of debate (Gordon et al., 2014; Yeo et al., 2011), evidence suggests substantial overlaps between the *dorsal executive* and *ventral affective* systems identified by investigations of emotion-cognition interactions (Iordan et al., 2013) and the central-executive and salience networks, respectively. The default-mode network has been implicated in various functions linked to emotion, such as retrieval of personally-significant memories and self-regulation (Cabeza and St Jacques, 2007; Denkova et al., 2015; Iordan et al., 2019). In this view, the enhancing and impairing effects of emotion may emerge from synergistic or antagonistic interactions among the large-scale brain networks. Among these networks, the *salience network* appears to most reliably track the emotional response (Lindquist and Barrett, 2012). However, executive aspects of processing involved in the response to emotional distraction (e.g., coping with distraction) seem to involve the cingulo-opercular network, which is anchored in the fronto-insular and anterior cingulate cortices (Gordon et al., 2014). Clarification of these overlaps and dissociations warrants further research.

4 Separation into functional domains subserved by the salience and executive control networks also provides a useful framework for better understanding adaptive changes in behavior associated with the impact of stress on cognition, at different time scales (Hermans et al., 2014). According to this model, in the acute stress phase, up-regulation of the salience network and suppression of the executive control network promotes rapid responses essential for short-time survival, such as fear and vigilance, based on more rigid patterns of behavior, and at the expense of elaborate cognitive control (Hermans et al., 2011). After the stressor subsides, during the recovery phase, a reverse shift occurs which promotes normalization of emotional reactivity and enhancement of higher-order cognition, important for long-term survival (Henckens et al., 2011). Hence, investigating the conditions leading to the recruitment of the salience network in conjunction or in conflict with the other brain networks provides a promising avenue for determining links and dissociations between the opposing effects of emotion and their relevance for psychopathology (Menon, 2011; Sylvester et al., 2012; Uddin, 2014).

5 Furthermore, comparing the brain mechanisms engaged by emotional distraction would potentially allow a more fine-grained dissociation between the network components of the dorsal-executive and ventral-affective neural systems, in the context of active task performance. Although the study of large-scale neural networks (e.g., Dosenbach et al., 2007; Power and Petersen, 2013; Seeley et al., 2007; Yeo et al., 2011) has become possible as a result of assessing resting-state functional connectivity, this method has limited ability to capture dynamic interactions among these networks, and thus it provides only a "static picture" of their connectivity. By contrast, specific task manipulations used by studies of emotion-cognition interactions (reviewed in Dolcos et al., 2011; Iordan et al., 2013) have proven effective in eliciting active dissociations among the major brain networks. Hence, such dual tasks with cognitive/ executive and emotional components provide a useful way of studying active interactions between the large-scale brain networks. For instance, there is evidence suggesting that the salience network mediates the interactions between the fronto-parietal and default-mode networks (Di and Biswal, 2013; Goulden et al., 2014). Biasing toward processing of internal or external information by manipulating the originating source of emotion in the context of dual cognitive-emotional tasks (e.g., Iordan et al., 2019) could provide a direct way of testing this hypothesis. Investigation of these networks could also benefit from the employment of novel approaches designed for enhanced interpretability and effectiveness at relatively limited sample sizes of the typical fMRI studies (Bogdan et al., 2023b).

6 Finally, future investigations of the brain mechanisms involved in the response to and coping with emotional distraction in both healthy and clinical populations would benefit from considering not only distracters coming from the outside world (*external* distraction) but also distracters originating from the internal environment, such as memories or thoughts about distressing events (*internal* distraction). Although previous investigations by us and by others (reviewed in Dolcos et al., 2011; Iordan et al., 2013) provided basic evidence concerning the behavioral and brain mechanisms by which irrelevant emotions interfere with on-going cognitive performance, they focused only on the effects of external distraction, such as emotional pictures, and thus it is unclear whether internal distraction produces similar effects. This issue is important because cognitive interference can be elicited also internally (Smallwood and Schooler, 2006), and is exacerbated

> in affective disturbances (Dolcos, 2013). Hence, clarifying the role of the internal environment in the impact of emotional distraction on cognitive processing could provide insights into the mechanisms of cognitive interference produced in affective disorders by rumination on distressing memories (Cooney et al., 2010; Nolen-Hoeksema, 1991), which can act as a potent internally-generated emotional distraction (Iordan et al., 2019). Notably, training programs that involve exposure to both internal and external emotional challenges provide the opportunity to strengthen emotion regulation and coping strategies, which can result in increased resilience and well-being (Dolcos et al., 2021). The effectiveness of such training programs could be further increased by complementing them with neuromodulation interventions targeting key brain regions identified by neuroimaging studies (Dolcos et al., 2021; Bogdan et al., 2024).

Overall, the present review emphasizes the need to consider the various factors that can influence opposing effects of emotion on cognition and identifies new avenues for future investigations of emotion-cognition interactions. These issues have relevance for understanding mechanisms of emotion-cognition interactions in healthy functioning and in clinical condition where such opposing effects of emotion tend to be exacerbated and deleterious. The ultimate goal of research in this field is identification of the factors that allow for optimal emotion-cognition interactions, which result in happy, healthy, and productive lives.

Author contributions

FD: Writing – original draft, Writing – review & editing. ED: Writing – original draft. AI: Writing – original draft. AS: Writing – original draft. GF: Writing – review & editing. SD: Writing – original draft, Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. FD was supported by an Emanuel Donchin Professorial Scholarship in Psychology, from the University of Illinois.

Acknowledgments

This work was conducted in part at the Biomedical Imaging Center of the Beckman Institute for Advanced Science & Technology at the University of Illinois at UrbanaChampaign (UIUC-BI-BI).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

References

Abercrombie, E. D., Keefe, K. A., DiFrischia, D. S., and Zigmond, M. J. (1989). Differential effect of stress on in vivo dopamine release in striatum, nucleus accumbens, and medial frontal cortex. *J. Neurochem.* 52, 1655–1658. doi: 10.1111/j.1471-4159.1989.tb09224.x

Adolphs, R., Tranel, D., and Buchanan, T. W. (2005). Amygdala damage impairs emotional memory for gist but not details of complex stimuli. Nat. Neurosci. 8, 512–518. doi: 10.1038/nn1413

Amaral, D. G., Behniea, H., and Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience* 118, 1099–1120. doi: 10.1016/S0306-4522(02)01001-1

Anand, A., Li, Y., Wang, Y., Gardner, K., and Lowe, M. J. (2007). Reciprocal effects of antidepressant treatment on activity and connectivity of the mood regulating circuit: an FMRI study. *J. Neuropsychiatr. Clin. Neurosci.* 19, 274–282. doi: 10.1176/jnp.2007.19.3.274

Anderson, A. K., and Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature* 411, 305–309. doi: 10.1038/35077083

Anderson, E., Siegel, E. H., and Barrett, L. F. (2011). What you feel influences what you see: the role of affective feelings in resolving binocular rivalry. *J. Exp. Soc. Psychol.* 47, 856–860. doi: 10.1016/j.jesp.2011.02.009

Arnsten, A. F. (1998). The biology of being frazzled. *Science* 280, 1711–1712. doi: 10.1126/science.280.5370.1711

Arnsten, A. F. (2000a). Stress impairs prefrontal cortical function in rats and monkeys: role of dopamine D1 and norepinephrine alpha-1 receptor mechanisms. *Prog. Brain Res.* 126, 183–192. doi: 10.1016/S0079-6123(00)26014-7

Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nat. Rev. Neurosci.* 10, 410–422. doi: 10.1038/nrn2648

Arnsten, A. F. T. (2000b). Through the looking glass: differential Noradenergic modulation of prefrontal cortical function. *Neural Plast.* 7, 133–146. doi: 10.1155/NP.2000.133

Aston-Jones, G., and Cohen, J. D. (2005). Adaptive gain and the role of the locus coeruleus–norepinephrine system in optimal performance. *J. Comp. Neurol.* 493, 99–110. doi: 10.1002/cne.20723

Benau, E. M., Orloff, N. C., Janke, E. A., Serpell, L., and Timko, C. A. (2014). A systematic review of the effects of experimental fasting on cognition☆. *Appetite* 77, 52–61. doi: 10.1016/j.appet.2014.02.014

Berkers, R. M., Klumpers, F., and Fernandez, G. (2016). Medial prefrontal-hippocampal connectivity during emotional memory encoding predicts individual differences in the loss of associative memory specificity. *Neurobiol. Learn. Mem.* 134, 44–54. doi: 10.1016/j.nlm.2016.01.016

Birnbaum, S., Gobeske, K. T., Auerbach, J., Taylor, J. R., and Arnsten, A. F. T. (1999). A role for norepinephrine in stress-induced cognitive deficits: α-1-adrenoceptor mediation in the prefrontal cortex. *Biol. Psychiatry* 46, 1266–1274. doi: 10.1016/S0006-3223(99)00138-9

Bisby, J. A., Burgess, N., and Brewin, C. R. (2020). Reduced memory coherence for negative events and Its relationship to posttraumatic stress disorder. Curr. Dir. Psychol. Sci. 29, 267–272. doi: 10.1177/0963721420917691

Bisby, J. A., Horner, A. J., Horlyck, L. D., and Burgess, N. (2016). Opposing effects of negative emotion on amygdalar and hippocampal memory for items and associations. *Soc. Cogn. Affect. Neurosci.* 11, 981–990. doi: 10.1093/scan/nsw028

Bisby, J., and Burgess, N. (2017). Differential effects of negative emotion on memory for items and associations, and their relationship to intrusive imagery. *Curr. Opin. Behav. Sci.* 17, 124–132. doi: 10.1016/j.cobeha.2017.07.012

Blaney, P. H. (1986). Affect and memory: a review. *Psychol. Bull.* 99, 229–246. doi: 10.1037/0033-2909.99.2.229

Bocanegra, B. R., and Zeelenberg, R. (2009a). Dissociating emotion-induced blindness and hypervision. *Emotion* 9, 865–873. doi: 10.1037/a0017749

Bocanegra, B. R., and Zeelenberg, R. (2009b). Emotion improves and impairs early vision. *Psychol. Sci.* 20, 707–713. doi: 10.1111/j.1467-9280.2009.02354.x

Bocanegra, B. R., and Zeelenberg, R. (2011a). Emotion-induced trade-offs in spatiotemporal vision. *J. Exp. Psychol. Gen.* 140, 272–282. doi: 10.1037/a0023188

Bocanegra, B. R., and Zeelenberg, R. (2011b). Emotional cues enhance the attentional effects on spatial and temporal resolution. *Psychon. Bull. Rev.* 18, 1071–1076. doi: 10.3758/s13423-011-0156-z

Bogdan, P. C., Dolcos, F., Katsumi, Y., O'Brien, M., Iordan, A. D., Iwinski, S., et al. (2024). Reconciling opposing effects of emotion on relational memory: behavioral, eye-tracking, and brain imaging investigations. *J. Exp. Psychol. Gen.* 153, 3074–3106. doi: 10.1037/xge0001625

Bogdan, P. C., Dolcos, S., Federmeier, F., Lleras, A., Schwarb, H., and Dolcos, F. (2023a). Emotional dissociations in temporal associations: opposing effects of arousal on memory for details surrounding unpleasant events. *Cognit. Emot.* 22, 1–15. doi: 10.1080/02699931.2023.2270196

Bogdan, P. C., Iordan, A. D., Shobrook, J., and Dolcos, F. (2023b). ConnSearch: a framework for functional connectivity analysis designed for interpretability and effectiveness at limited sample sizes. *NeuroImage* 278:120274. doi: 10.1016/j.neuroimage.2023.120274

Bowen, H. J., Kark, S. M., and Kensinger, E. A. (2018). NEVER forget: negative emotional valence enhances recapitulation. Psychon. Bull. Rev. 25, 870–891. doi: 10.3758/s13423-017-1313-9

Bressler, S. L., and Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and principles. *Trends Cogn. Sci.* 14, 277–290. doi: 10.1016/j.tics.2010.04.004

Brown, M. W., and Aggleton, J. P. (2001). Recognition memory: what are the roles of the perirhinal cortex and hippocampus? *Nat. Rev. Neurosci.* 2, 51–61. doi: 10.1038/35049064

Brown, V. M., and Morey, R. A. (2012). Neural systems for cognitive and emotional processing in posttraumatic stress disorder. *Front. Psychol.* 3:449. doi: 10.3389/fpsyg.2012.00449

Buetti, S., and Lleras, A. (2012). Perceiving control over aversive and fearful events can alter how we experience those events: an investigation of time perception in spider-fearful individuals. *Front. Psychol.* 3:337. doi: 10.3389/fpsyg.2012.00337

Butts, K. A., Weinberg, J., Young, A. H., and Phillips, A. G. (2011). Glucocorticoid receptors in the prefrontal cortex regulate stress-evoked dopamine efflux and aspects of executive function. *Proc. Natl. Acad. Sci. USA* 108, 18459–18464. doi: 10.1073/pnas.1111746108

Cabeza, R., and St Jacques, P. (2007). Functional neuroimaging of autobiographical memory. *Trends Cogn. Sci.* 11, 219–227. doi: 10.1016/j.tics.2007.02.005

Calbi, M., Montalti, M., Pederzani, C., Arcuri, E., Umiltà, M. A., Gallese, V., et al. (2022). Emotional body postures affect inhibitory control only when task-relevant. *Front. Psychol.* 13:1035328. doi: 10.3389/fpsyg.2022.1035328

Canli, T. (2004). Functional brain mapping of extraversion and neuroticism: learning from individual differences in emotion processing. *J. Pers.* 72, 1105–1132. doi: 10.1111/j.1467-6494.2004.00292.x

Charles, S. T., Mather, M., and Carstensen, L. L. (2003). Aging and emotional memory: the forgettable nature of negative images for older adults. *J. Exp. Psychol. Gen.* 132, 310–324. doi: 10.1037/0096-3445.132.2.310

Chiu, Y. C., Dolcos, F., Gonsalves, B. D., and Cohen, N. J. (2013). On opposing effects of emotion on contextual or relational memory. *Front. Psychol.* 4:103. doi: 10.3389/fpsyg.2013.00103

Christianson, S. A. (1992). Emotional stress and eyewitness memory: a critical review. *Psychol. Bull.* 112, 284–309. doi: 10.1037/0033-2909.112.2.284

Ciesielski, B. G., Armstrong, T., Zald, D. H., and Olatunji, B. O. (2010). Emotion modulation of visual attention: categorical and temporal characteristics. *PLoS One* 5:e13860. doi: 10.1371/journal.pone.0013860

Clarke, R., and Johnstone, T. (2013). Prefrontal inhibition of threat processing reduces working memory interference. *Front. Hum. Neurosci.* 7:228. doi: 10.3389/fnhum.2013.00228

Cohen, A. O., Dellarco, D. V., Breiner, K., Helion, C., Heller, A. S., Rahdar, A., et al. (2016). The impact of emotional states on cognitive control circuitry and function. *J. Cogn. Neurosci.* 28, 446–459. doi: 10.1162/jocn_a_00906

Cohen, N. J., and Eichenbaum, H. (1993). Memory, amnesia and the hippocampal system. Cambridge, MA: The MIT Press.

Cohen, N. J., Ryan, J., Hunt, C., Romine, L., Wszalek, T., and Nash, C. (1999). Hippocampal system and declarative (relational) memory: summarizing the data from functional neuroimaging studies. *Hippocampus* 9, 83–98. doi: 10.1002/(SICI)1098-1063(1999)9:1<83::AID-HIPO9>3.0.CO;2-7

Cooney, R. E., Joormann, J., Eugene, F., Dennis, E. L., and Gotlib, I. H. (2010). Neural correlates of rumination in depression. *Cognive Aff. Behav. Neurosci.* 10, 470–478. doi: 10.3758/CABN.10.4.470

Corbetta, M., and Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215. doi: 10.1038/nrn755nrn755

Davachi, L., Mitchell, J. P., and Wagner, A. D. (2003). Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *Proc. Natl. Acad. Sci. USA* 100, 2157–2162. doi: 10.1073/pnas.0337195100

Davidson, R. J., Irwin, W., Anderle, M. J., and Kalin, N. H. (2003). The neural substrates of affective processing in depressed patients treated with venlafaxine. *Am. J. Psychiatry* 160, 64–75. doi: 10.1176/appi.ajp.160.1.64

de Kloet, E. R., Joels, M., and Holsboer, F. (2005). Stress and the brain: from adaptation to disease. *Nat. Rev. Neurosci.* 6, 463–475. doi: 10.1038/nrn1683

Denkova, E., Dolcos, S., and Dolcos, F. (2015). Neural correlates of 'distracting' from emotion during autobiographical recollection. *Soc. Cogn. Affect. Neurosci.* 10, 219–230. doi: 10.1093/scan/nsu039

de Terte, I., and Stephens, C. (2014). Psychological resilience of workers in high-risk occupations. *Stress. Health* 30, 353–355. doi: 10.1002/smi.2627

Diamond, D. M., Campbell, A. M., Park, C. R., Halonen, J., and Zoladz, P. R. (2007). The temporal dynamics model of emotional memory processing: a synthesis on the neurobiological basis of stress-induced amnesia, flashbulb and traumatic memories, and the Yerkes-Dodson law. *Neural Plast.* 2007:60803. doi: 10.1155/2007/60803

Dillon, D. G., Ritchey, M., Johnson, B. D., and LaBar, K. S. (2007). Dissociable effects of conscious emotion regulation strategies on explicit and implicit memory. *Emotion* 7, 354–365. doi: 10.1037/1528-3542.7.2.354

Di, X., and Biswal, B. B. (2013). Modulatory interactions between the default mode network and task positive networks in resting-state. *PeerJ* 2:e367. doi: 10.7717/peerj.367

Dolcos, F. (2013). Linking enhancing and impairing effects of emotion – the case of PTSD. *Front. Integr. Neurosci.* 7:26. doi: 10.3389/fnint.2013.00026

Dolcos, F. (2014). The fast and the slow sides of cortisol's effects on emotional interference and sustained attention. *Front. Neurosci.* 8:268. doi: 10.3389/fnins.2014.00268

Dolcos, F., and Denkova, E. (2008). Neural correlates of encoding emotional memories: a review of functional neuroimaging evidence. *Cell Sci. Rev.* 5, 78–122.

Dolcos, F., Denkova, E., and Dolcos, S. (2012). Neural correlates of emotional memories: a review of evidence from brain imaging studies. *Psychologia* 55, 80–111. doi: 10.2117/psysoc.2012.80

Dolcos, F., Diaz-Granados, P., Wang, L., and McCarthy, G. (2008). Opposing influences of emotional and non-emotional distracters upon sustained prefrontal cortex activity during a delayed-response working memory task. *Neuropsychologia* 46, 326–335. doi: 10.1016/j.neuropsychologia.2007.07.010

Dolcos, F., Iordan, A. D., and Dolcos, S. (2011). Neural correlates of emotion-cognition interactions: a review of evidence from brain imaging investigations. *J. Cogn. Psychol.* 23, 669–694. doi: 10.1080/20445911.2011.594433

Dolcos, F., Iordan, A., Kragel, J., Stokes, J., Campbell, R., McCarthy, G., et al. (2013). Neural correlates of opposing effects of emotional distraction on working memory and episodic memory: an event related fMRI investigation. *Front. Psychol.* 4:293. doi: 10.3389/fpsyg.2013.00293

Dolcos, F., Katsumi, Y., Bogdan, P. C., Shen, C., Jun, S., Buetti, S., et al. (2020a). The impact of focused attention on subsequent emotional recollection: a functional MRI investigation. *Neuropsychologia* 138:107338. doi: 10.1016/j.neuropsychologia.2020.107338

Dolcos, F., Katsumi, Y., Denkova, E., Weymar, M., and Dolcos, S. (2017a). Current issues and emerging directions in the impact of emotion on memory: a review of evidence from brain imaging investigations. *Memor. Soc. Context* 5, 57–107. doi: 10.1007/978-4-431-56591-8

Dolcos, F., Katsumi, Y., Shen, C., Bogdan, P. C., Jun, S., Larsen, R., et al. (2020b). The impact of focused attention on emotional experience: a functional MRI investigation. *Cogn. Affect. Behav. Neurosci.* 20, 1011–1026. doi: 10.3758/s13415-020-00816-2

Dolcos, F., Katsumi, Y., Weymar, M., Moore, M., Tsukiura, T., and Dolcos, S. (2017b). Emerging directions in emotional episodic memory. *Front. Psychol. Emot. Sci.* 8:1867. doi: 10.3389/fpsyg.2017.01867

Dolcos, F., LaBar, K. S., and Cabeza, R. (2005). Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. Proc Natl Acad Sci USA. 102, 2626–2631. doi: 10.1073/pnas.0409848102

Dolcos, F., LaBar, K. S., and Cabeza, R. (2006). "The memory-enhancing effect of emotion: functional neuroimaging evidence" in Memory and emotion: Interdisciplinary perspectives. eds. B. Uttl, N. Ohta and A. L. Siegenthaler (Malden, MA: Blackwell Publishing), 107–133.

Dolcos, F., and McCarthy, G. (2006). Brain systems mediating cognitive interference by emotional distraction. *J. Neurosci.* 26, 2072–2079. doi: 10.1523/JNEUROSCI.5042-05.2006

Dolcos, F., Miller, B., Kragel, P., Jha, A., and McCarthy, G. (2007). Regional brain differences in the effect of distraction during the delay interval of a working memory task. *Brain Res.* 1152, 171–181. doi: 10.1016/j.brainres.2007.03.059

Dolcos, F., and Talmi, D. (2024). “Reconciling the impact of emotion on episodic relational memory,” in *Symposium conducted at the annual meeting of the Cognitive Neuroscience Society. Cognitive Neuroscience Society*.

Dolcos, F., Wang, L., and Mather, M. (Eds.) (2015). “Current research and emerging directions in emotion cognition interactions” in the impact of emotion on cognition - dissociating between enhancing and impairing effects. Frontiers in integrative neuroscience and frontiers in psychology (Emotion Science). Frontiers Media SA. Available at: https://www.frontiersin.org/research-topics/704/the-impact-of-emotion-on-cognition---dissociating-between-enhancing-and-impairing-effects

Dolcos, S., Hu, Y., Williams, C., Bogdan, P. C., Hohl, K., Berenbaum, H., et al. (2021). Cultivating affective resilience: proof-of-principle evidence of translational benefits from a novel cognitive-emotional training intervention. *Front. Psychol.* 12:585536. doi: 10.3389/fpsyg.2021.585536

Dolcos, S., Katsumi, Y., and Dixon, R. A. (2014). The role of arousal in the spontaneous regulation of emotions in healthy aging: a fMRI investigation. *Front. Psychol.* 5:681. doi: 10.3389/fpsyg.2014.00681

Dosenbach, N. U., Fair, D. A., Cohen, A. L., Schlaggar, B. L., and Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends Cogn. Sci.* 12, 99–105. doi: 10.1016/j.tics.2008.01.001

Dosenbach, N. U., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A., et al. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proc. Nat. Acad. Sci. USA* 104, 11073–11078. doi: 10.1073/pnas.0704320104

Dosenbach, N., Visscher, K., Palmer, E., Miezin, F., Wenger, K., Kang, H., et al. (2006). A core system for the implementation of task sets. *Neuron* 50, 799–812. doi: 10.1016/j.neuron.2006.04.031

Dougal, S., Phelps, E. A., and Davachi, L. (2007). The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cogn. Affect. Behav. Neurosci.* 7, 233–242. doi: 10.3758/CABN.7.3.233

Drevets, W. C. (2001). Neuroimaging and neuropathological studies of depression: implications for the cognitive-emotional features of mood disorders. *Curr. Opin. Neurobiol.* 11, 240–249. doi: 10.1016/S0959-4388(00)00203-8

Dux, P. E., and Marois, R. (2009). The attentional blink: a review of data and theory. *Atten. Percept. Psychophys.* 71, 1683–1700. doi: 10.3758/APP.71.8.1683

Eichenbaum, H., and Cohen, N. J. (2001). From conditioning to conscious recollection: Memory Systems of the Brain. New York, NY: Oxford University Press.

Everaerd, D., Klumpers, F., van Wingen, G., Tendolkar, I., and Fernandez, G. (2015). Association between neuroticism and amygdala responsivity emerges under stressful conditions. *NeuroImage* 112, 218–224. doi: 10.1016/j.neuroimage.2015.03.014

Ezzyat, Y., and Davachi, L. (2014). Similarity breeds proximity: pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron* 81, 1179–1189. doi: 10.1016/j.neuron.2014.01.042

Fitzgerald, D. A., Arnold, J. F., Becker, E. S., Speckens, A. E., Rinck, M., Rijpkema, M., et al. (2011). How mood challenges emotional memory formation: an fMRI investigation. *NeuroImage* 56, 1783–1790. doi: 10.1016/j.neuroimage.2011.02.061

Fitzgerald, P. B., Laird, A. R., Maller, J., and Daskalakis, Z. J. (2008). A meta-analytic study of changes in brain activation in depression. *Hum. Brain Mapp.* 29, 683–695. doi: 10.1002/hbm.20426

Foote, S. L., and Morrison, J. H. (1987). Extrathalamic modulation of cortical function. *Annu. Rev. Neurosci.* 10, 67–95. doi: 10.1146/annurev.ne.10.030187.000435

Fu, C. H., Williams, S. C., Cleare, A. J., Brammer, M. J., Walsh, N. D., Kim, J., et al. (2004). Attenuation of the neural response to sad faces in major depression by antidepressant treatment: a prospective, event-related functional magnetic resonance imaging study. *Arch. Gen. Psychiatry* 61, 877–889. doi: 10.1001/archpsyc.61.9.877

Gordon, E. M., Laumann, T. O., Adeyemo, B., Huckins, J. F., Kelley, W., and Petersen, S. E. (2014). Generation and evaluation of a cortical area Parcellation from resting-state correlations. *Cereb. Cortex* 26, 288–303. doi: 10.1093/cercor/bhu239

Gotlib, I. H., Sivers, H., Gabrieli, J. D., Whitfield-Gabrieli, S., Goldin, P., Minor, K. L., et al. (2005). Subgenual anterior cingulate activation to valenced emotional stimuli in major depression. *Neuroreport* 16, 1731–1734. doi: 10.1097/01.wnr.0000183901.70030.82

Goulden, N., Khusnulina, A., Davis, N. J., Bracewell, R. M., Bokde, A. L., McNulty, J. P., et al. (2014). The salience network is responsible for switching between the default mode network and the central executive network: replication from DCM. *NeuroImage* 99, 180–190. doi: 10.1016/j.neuroimage.2014.05.052

Graf, P., and Schacter, D. L. (1989). Unitization and grouping mediate dissociations in memory for new associations. *J. Exp. Psychol. Learn. Mem. Cogn.* 15, 930–940.

Greene, C. M., Flannery, O., and Soto, D. (2014). Distinct parietal sites mediate the influences of mood, arousal, and their interaction on human recognition memory. *Cogn. Affect. Behav. Neurosci.* 14, 1327–1339. doi: 10.3758/s13415-014-0266-y

Gross, J. J., Carstensen, L. L., Pasupathi, M., Tsai, J., Skorpen, C. G., and Hsu, A. Y. (1997). Emotion and aging: experience, expression, and control. *Psychol. Aging* 12, 590–599. doi: 10.1037/0882-7974.12.4.590

Grühn, D., Scheibe, S., and Baltes, P. B. (2007). Reduced negativity effect in older adults’ memory for emotional pictures: the heterogeneity–homogeneity list paradigm. *Psychol. Aging* 22, 644–649. doi: 10.1037/0882-7974.22.3.644

Gunthert, K. C., Cohen, L. H., and Armeli, S. (1999). The role of neuroticism in daily stress and coping. *J. Pers. Soc. Psychol.* 77, 1087–1100. doi: 10.1037/0022-3514.77.5.1087

Gutchess, A. H., Kensinger, E. A., and Schacter, D. L. (2007). Aging, self-referencing, and medial prefrontal cortex. *Soc. Neurosci.* 2, 117–133. doi: 10.1080/17470910701399029

Hains, A. B., and Arnsten, A. F. (2008). Molecular mechanisms of stress-induced prefrontal cortical impairment: implications for mental illness. *Learn. Mem.* 15, 551–564. doi: 10.1101/lm.921708

Harvey, P. O., Fossati, P., Pochon, J. B., Levy, R., Lebastard, G., Lehericy, S., et al. (2005). Cognitive control and brain resources in major depression: an fMRI study using the n-back task. *NeuroImage* 26, 860–869. doi: 10.1016/j.neuroimage.2005.02.048

Hayes, J. P., LaBar, K. S., McCarthy, G., Selgrade, E., Nasser, J., Dolcos, F., et al. (2011). Reduced hippocampal and amygdala activity predicts memory distortions for trauma reminders in combat-related PTSD. *J. Psychiatr. Res.* 45, 660–669. doi: 10.1016/j.jpsychires.2010.10.007

Hayes, J. P., VanElzakker, M. B., and Shin, L. M. (2012). Emotion and cognition interactions in PTSD: a review of neurocognitive and neuroimaging studies. *Front. Integr. Neurosci.* 6:89. doi: 10.3389/fnint.2012.00089

Henckens, M. J., van Wingen, G. A., Joels, M., and Fernandez, G. (2010). Time-dependent effects of corticosteroids on human amygdala processing. *J. Neurosci.* 30, 12725–12732. doi: 10.1523/JNEUROSCI.3112-10.2010

Henckens, M. J., van Wingen, G. A., Joels, M., and Fernandez, G. (2011). Time-dependent corticosteroid modulation of prefrontal working memory processing. *Proc. Natl. Acad. Sci. USA* 108, 5801–5806. doi: 10.1073/pnas.1019128108

Henckens, M. J., van Wingen, G. A., Joels, M., and Fernandez, G. (2012). Time-dependent effects of cortisol on selective attention and emotional interference: a functional MRI study. *Front. Integr. Neurosci.* 6:66. doi: 10.3389/fnint.2012.00066

Henckens, M. J., van Wingen, G. A., Joëls, M., and Fernández, G. (2012). Corticosteroid induced decoupling of the amygdala in men. *Cereb. Cortex* 22, 2336–2345. doi: 10.1093/cercor/bhr313

Henderson, R. K., Snyder, H. R., Gupta, T., and Banich, M. T. (2012). When does stress help or harm? The effects of stress controllability and subjective stress response on Stroop performance. *Front. Psychol.* 3:179. doi: 10.3389/fpsyg.2012.00179

Hermans, E. J., Henckens, M. J. A. G., Joëls, M., and Fernández, G. (2014). Dynamic adaptation of large-scale brain networks in response to acute stressors. *Trends Neurosci.* 37, 304–314. doi: 10.1016/j.tins.2014.03.006

Hermans, E. J., Marle, H. J. F. V., Ossewaarde, L., Henckens, M. J. A. G., Qin, S., Kesteren, M. T. R. V., et al. (2011). Stress-related noradrenergic activity prompts large-scale neural network reconfiguration. *Science (New York, N.Y.)* 334, 1151–1153. doi: 10.1126/science.1209603

Hirsch, C. R., and Mathews, A. (2012). A cognitive model of pathological worry. *Behav. Res. Ther.* 50, 636–646. doi: 10.1016/j.brat.2012.06.007

Iordan, A. D., Dolcos, S., and Dolcos, F. (2013). Neural signatures of the response to emotional distraction: a review of evidence from brain imaging investigations. *Front. Hum. Neurosci.* 7:200. doi: 10.3389/fnhum.2013.00200

Iordan, A. D., Dolcos, S., and Dolcos, F. (2019). Brain activity and network interactions in the impact of internal emotional distraction. *Cereb. Cortex* 29, 2607–2623. doi: 10.1093/cercor/bhy129

Isaacowitz, D. M., Wadlinger, H. A., Goren, D., and Wilson, H. R. (2006). Is there an age-related positivity effect in visual attention? A comparison of two methodologies. *Emotion* 6, 511–516. doi: 10.1037/1528-3542.6.3.511

Jha, A. P., Morrison, A. B., Dainer-Best, J., Parker, S., Rostrup, N., and Stanley, E. A. (2015). Minds "at attention": mindfulness training curbs attentional lapses in military cohorts. *PLoS One* 10:e0116889. doi: 10.1371/journal.pone.0116889

Jha, A. P., Stanley, E. A., Kiyonaga, A., Wong, L., and Gelfand, L. (2010). Examining the protective effects of mindfulness training on working memory capacity and affective experience. *Emotion* 10, 54–64. doi: 10.1037/a0018438

Joels, M., and Baram, T. Z. (2009). The neuro-symphony of stress. *Nat. Rev. Neurosci.* 10, 459–466. doi: 10.1038/nrn2632

Joels, M., Sarabdjitsingh, R. A., and Karst, H. (2012). Unraveling the time domains of corticosteroid hormone influences on brain activity: rapid, slow, and chronic modes. *Pharmacol. Rev.* 64, 901–938. doi: 10.1124/pr.112.005892

Johnstone, M., and Feeney, J. (2015). Individual differences in responses to workplace stress: the contribution of attachment theory. *J. Appl. Soc. Psychol.* 45, 412–424. doi: 10.1111/jasp.12308

Jorm, A. F. (2000). Does old age reduce the risk of anxiety and depression? A review of epidemiological studies across the adult life span. *Psychol. Med.* 30, 11–22. doi: 10.1017/S0033291799001452

Kaplan, J. B., Bergman, A. L., Christopher, M., Bowen, S., and Hunsinger, M. (2017). Role of resilience in mindfulness training for first responders. *Mindfulness* 8, 1373–1380. doi: 10.1007/s12671-017-0713-2

Karst, H., and Joëls, M. (2005). Corticosterone slowly enhances miniature excitatory postsynaptic current amplitude in mice CA1 hippocampal cells. *J. Neurophysiol.* 94, 3479–3486. doi: 10.1152/jn.00143.2005

Keightley, M. L., Winocur, G., Graham, S. J., Mayberg, H. S., Hevenor, S. J., and Grady, C. L. (2003). An fMRI study investigating cognitive modulation of brain regions associated with emotional processing of visual stimuli. *Neuropsychologia* 41, 585–596. doi: 10.1016/S0028-3932(02)00199-9

Keil, A., and Ihssen, N. (2004). Identification facilitation for emotionally arousing verbs during the attentional blink. *Emotion* 4, 23–35. doi: 10.1037/1528-3542.4.1.23

Kensinger, E. A. (2009). Remembering the details: effects of emotion. *Emot. Rev.* 1, 99–113. doi: 10.1177/1754073908100432

Kensinger, E. A., Garoff-Eaton, R. J., and Schacter, D. L. (2007a). Effects of emotion on memory specificity: memory trade-offs elicited by negative visually arousing stimuli. *J. Mem. Lang.* 56, 575–591. doi: 10.1016/j.jml.2006.05.004

Kensinger, E. A., Garoff-Eaton, R. J., and Schacter, D. L. (2007b). How negative emotion enhances the visual specificity of a memory. *J. Cogn. Neurosci.* 19, 1872–1887. doi: 10.1162/jocn.2007.19.11.1872

Kensinger, E. A., and Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *J. Neurosci.* 26, 2564–2570. doi: 10.1523/JNEUROSCI.5241-05.2006

Kensinger, E. A., and Schacter, D. L. (2008). Neural processes supporting young and older adults' emotional memories. *J. Cogn. Neurosci.* 20, 1161–1173. doi: 10.1162/jocn.2008.20080

Kerr, D. L., McLaren, D. G., Mathy, R. M., and Nitschke, J. B. (2012). Controllability modulates the anticipatory response in the human ventromedial prefrontal cortex. *Front. Psychol.* 3:557. doi: 10.3389/fpsyg.2012.00557

Khawli, E. E., Fan, Y., Aust, S., Wirth, K., Bonke, L., Stevense, A., et al. (2017). Early-life stress modulates neural networks associated with habitual use of reappraisal. *Behav. Brain Res.* 337, 210–217. doi: 10.1016/j.bbr.2017.09.018

Killgore, W. D. S. (2010). "Effects of sleep deprivation on cognition" in Progress in brain research. eds. G. A. Kerkhof and H. P. A. V. Dongen (Amsterdam: Elsevier), 105–129.

Koster, E. H., De Raedt, R., Goeleven, E., Franck, E., and Crombez, G. (2005). Mood-congruent attentional bias in dysphoria: maintained attention to and impaired disengagement from negative information. *Emotion* 5, 446–455. doi: 10.1037/1528-3542.5.4.446

Krause, A. J., Simon, E. B., Mander, B. A., Greer, S. M., Saletin, J. M., Goldstein-Piekarski, A. N., et al. (2017). The sleep-deprived human brain. *Nat. Rev. Neurosci.* 18, 404–418. doi: 10.1038/nrn.2017.55

Kryla-Lighthall, N., and Mather, M. (2009). "The role of cognitive control in older adults' emotional well-being" in Handbook of theories of aging. eds. V. Berngtson, D. Gans, N. Putney and M. Silverstein. *2nd* ed (Cham: Springer Publishing), 323–344.

Ladouceur, C. D. (2012). Neural systems supporting cognitive-affective interactions in adolescence: the role of puberty and implications for affective disorders. *Front. Integr. Neurosci.* 6:65. doi: 10.3389/fnint.2012.00065

Leclerc, C. M., and Kensinger, E. A. (2008). Age-related differences in medial prefrontal activation in response to emotional images. *Cogn. Affect. Behav. Neurosci.* 8, 153–164. doi: 10.3758/CABN.8.2.153

Lee, T. H., Itti, L., and Mather, M. (2012). Evidence for arousal-biased competition in perceptual learning. *Front. Psychol.* 3:241. doi: 10.3389/fpsyg.2012.00241

Lee, T. H., Sakaki, M., Cheng, R., Velasco, R., and Mather, M. (2014). Emotional arousal amplifies the effects of biased competition in the brain. *Soc. Cogn. Affect. Neurosci.* 9, 2067–2077. doi: 10.1093/scan/nsu015

Levine, L. J., and Edelstein, R. S. (2009). Emotion and memory narrowing: a review and goal-relevance approach. *Cognit. Emot.* 23, 833–875. doi: 10.1080/02699930902738863

Lewis, P. A., Critchley, H. D., Smith, A. P., and Dolan, R. J. (2005). Brain mechanisms for mood congruent memory facilitation. *NeuroImage* 25, 1214–1223. doi: 10.1016/j.neuroimage.2004.11.053

Lim, S. L., Padmala, S., and Pessoa, L. (2009). Segregating the significant from the mundane on a moment-to-moment basis via direct and indirect amygdala contributions. *Proc. Natl. Acad. Sci. USA* 106, 16841–16846. doi: 10.1073/pnas.0904551106

Lindquist, K., and Barrett, L. (2012). A functional architecture of the human brain: emerging insights from the science of emotion. *Trends Cogn. Sci.* 16, 533–540. doi: 10.1016/j.tics.2012.09.005

Loftus, E. F., Loftus, G. R., and Messo, J. (1987). Some facts about "weapon focus". *Law Hum. Behav.* 11, 55–62. doi: 10.1007/BF01044839

Luo, Q., Holroyd, T., Majestic, C., Cheng, X., Schechter, J., and Blair, R. J. (2010). Emotional automaticity is a matter of timing. *J. Neurosci.* 30, 5825–5829. doi: 10.1523/JNEUROSCI.BC-5668-09.2010

Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., and Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: implications for the field of brain and cognition. *Brain Cogn.* 65, 209–237. doi: 10.1016/j.bandc.2007.02.007

Lupien, S. J., McEwen, B. S., Gunnar, M. R., and Heim, C. (2009). Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Nat. Rev. Neurosci.* 10, 434–445. doi: 10.1038/nrn2639

Mancini, C., Falciati, L., Maioli, C., and Mirabella, G. (2022). Happy facial expressions impair inhibitory control with respect to fearful facial expressions but only when task-relevant. *Emotion* 22, 142–152. doi: 10.1037/emo0001058

Mather, M. (2007). Emotional arousal and memory binding: an object-based framework. *Perspect. Psychol. Sci.* 2, 33–52. doi: 10.1111/j.1745-6916.2007.00028.x

Mather, M. (2012). The emotion paradox in the aging brain. *Ann. N. Y. Acad. Sci.* 1251, 33–49. doi: 10.1111/j.1749-6632.2012.06471.x

Mather, M., and Carstensen, L. L. (2003). Aging and attentional biases for emotional faces. *Psychol. Sci.* 14, 409–415. doi: 10.1111/1467-9280.01455

Mather, M., and Carstensen, L. L. (2005). Aging and motivated cognition: the positivity effect in attention and memory. *Trends Cogn. Sci.* 9, 496–502. doi: 10.1016/j.tics.2005.08.005

Mather, M., Clewett, D., Sakaki, M., and Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. Behav. Brain Sci. 39, e200. doi: 10.1017/S0140525X15000667

Mather, M., and Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspect. Psychol. Sci.* 6, 114–133. doi: 10.1177/1745691611400234

Matsuo, K., Glahn, D. C., Peluso, M. A., Hatch, J. P., Monkul, E. S., Najt, P., et al. (2007). Prefrontal hyperactivation during working memory task in untreated individuals with major depressive disorder. *Mol. Psychiatry* 12, 158–166. doi: 10.1038/sj.mp.4001894

Maunsell, J. H., Ghose, G. M., Assad, J. A., McAdams, C. J., Boudreau, C. E., and Noerager, B. D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Vis. Neurosci.* 16, 1–14. doi: 10.1017/S0952523899156177

Mayberg, H. S. (1997). Limbic-cortical dysregulation: a proposed model of depression. *J. Neuropsychiatr. Clin. Neurosci.* 9, 471–481. doi: 10.1176/jnp.9.3.471

Mayberg, H. S., Liotti, M., Brannan, S. K., McGinnis, S., Mahurin, R. K., Jerabek, P. A., et al. (1999). Reciprocal limbic-cortical function and negative mood: converging PET findings in depression and normal sadness. *Am. J. Psychiatry* 156, 675–682. doi: 10.1176/ajp.156.5.675

McEwen, B. S. (1998a). Protective and damaging effects of stress mediators. *N. Engl. J. Med.* 338, 171–179. doi: 10.1056/NEJM199801153380307

McEwen, B. S. (1998b). Stress, adaptation, and disease. Allostasis and allostatic load. *Ann. N. Y. Acad. Sci.* 840, 33–44. doi: 10.1111/j.1749-6632.1998.tb09546.x

McEwen, B. S. (2007). Physiology and neurobiology of stress and adaptation: central role of the brain. *Physiol. Rev.* 87, 873–904. doi: 10.1152/physrev.00041.2006

McEwen, B. S. (2016). In pursuit of resilience: stress, epigenetics, and brain plasticity. *Ann. N. Y. Acad. Sci.* 1373, 56–64. doi: 10.1111/nyas.13020

McGaugh, J. L. (2000). Memory-a century of consolidation. *Science* 287, 248–251. doi: 10.1126/science.287.5451.248

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annu. Rev. Neurosci.* 27, 1–28. doi: 10.1146/annurev.neuro.27.070203.144157

McGaugh, J. L. (2005). Emotional arousal and enhanced amygdala activity: new evidence for the old perseveration-consolidation hypothesis. *Learn. Mem.* 12, 77–79. doi: 10.1101/lm.93405

McHugo, M., Olatunji, B. O., and Zald, D. H. (2013). The emotional attentional blink: what we know so far. *Front. Hum. Neurosci.* 7:151. doi: 10.3389/fnhum.2013.00151

McReynolds, J. R., Donowho, K., Abdi, A., McGaugh, J. L., Roozendaal, B., and McIntyre, C. K. (2010). Memory-enhancing corticosterone treatment increases amygdala norepinephrine and arc protein expression in hippocampal synaptic fractions. *Neurobiol. Learn. Mem.* 93, 312–321. doi: 10.1016/j.nlm.2009.11.005

Menon, V. (2011). Large-scale brain networks and psychopathology: a unifying triple network model. *Trends Cogn. Sci.* 15, 483–506. doi: 10.1016/j.tics.2011.08.003

Mereu, S., and Lleras, A. (2013). Feelings of control restore distorted time perception of emotionally charged events. *Conscious. Cogn.* 22, 306–314. doi: 10.1016/j.concog.2012.08.004

Mickley Steinmetz, K. R., Scott, L. A., Smith, D., and Kensinger, E. A. (2012). The effects of trauma exposure and posttraumatic stress disorder (PTSD) on the emotion-induced memory trade-off. *Front. Integr. Neurosci.* 6:34. doi: 10.3389/fnint.2012.00034

Mirabella, G., Grassi, M., Mezzarobba, S., and Bernardis, P. (2023). Angry and happy expressions affect forward gait initiation only when task relevant. *Emotion* 23, 387–399. doi: 10.1037/emo0001112

Mirabella, G., Tullo, M. G., Sberna, G., and Galati, G. (2024). Context matters: task relevance shapes neural responses to emotional facial expressions. *Sci. Rep.* 14:17859. doi: 10.1038/s41598-024-68803-y

Montalti, M., and Mirabella, G. (2023). Unveiling the influence of task-relevance of emotional faces on behavioral reactions in a multi-face context using a novel flanker-go/no-go task. *Sci. Rep.* 13:20183. doi: 10.1038/s41598-023-47385-1

Morey, R. A., Dolcos, F., Petty, C. M., Cooper, D. A., Hayes, J. P., LaBar, K. S., et al. (2009). The role of trauma-related distractors on neural systems for working memory and emotion processing in posttraumatic stress disorder. *J. Psychiatr. Res.* 43, 809–817. doi: 10.1016/j.jpsychires.2008.10.014

Moscovitch, M., Cabeza, R., Winocur, G., and Nadel, L. (2016). Episodic memory and beyond: the Hippocampus and neocortex in transformation. *Annu. Rev. Psychol.* 67, 105–134. doi: 10.1146/annurev-psych-113011-143733

Most, S. B., Chun, M. M., Widders, D. M., and Zald, D. H. (2005). Attentional rubbernecking: cognitive control and personality in emotion-induced blindness. *Psychon. Bull. Rev.* 12, 654–661. doi: 10.3758/BF03196754

Nadel, L., and Jacobs, W. J. (1998). Traumatic memory is special. *Curr. Dir. Psychol. Sci.* 7, 154–157. doi: 10.1111/1467-8721.ep10836842

Nashiro, K., Sakaki, M., and Mather, M. (2012). Age differences in brain activity during emotion processing: reflections of age-related decline or increased emotion regulation? *Gerontology* 58, 156–163. doi: 10.1159/000328465

Nolen-Hoeksema, S. (1991). Responses to depression and their effects on the duration of depressive episodes. *J. Abnorm. Psychol.* 100, 569–582. doi: 10.1037/0021-843X.100.4.569

Ohman, A., Flykt, A., and Esteves, F. (2001a). Emotion drives attention: detecting the snake in the grass. *J. Exp. Psychol. Gen.* 130, 466–478. doi: 10.1037/0096-3445.130.3.466

Ohman, A., Lundqvist, D., and Esteves, F. (2001b). The face in the crowd revisited: a threat advantage with schematic stimuli. *J. Pers. Soc. Psychol.* 80, 381–396. doi: 10.1037/0022-3514.80.3.381

Olsson, A., and Öhman, A. (2009). "The affective neuroscience of emotion: automatic activation, Interoception, and emotion regulation" in Handbook of neuroscience for the behavioral sciences. eds. J. T. Cacioppo and G. G. Berntson (Hoboken, NJ: Wiley), 731–744.

Ormel, J., Jeronimus, B. F., Kotov, R., Riese, H., Bos, E. H., Hankin, B., et al. (2013). Neuroticism and common mental disorders: meaning and utility of a complex relationship. *Clin. Psychol. Rev.* 33, 686–697. doi: 10.1016/j.cpr.2013.04.003

Park, C. R., Campbell, A. M., Woodson, J. C., Smith, T. P., Fleshner, M., and Diamond, D. M. (2006). Permissive influence of stress in the expression of a U-shaped relationship between serum corticosterone levels and spatial memory errors in rats. *Dose Response* 4, 55–74. doi: 10.2203/dose-response.004.01.005.Park

Pessoa, L. (2013). The cognitive-emotional brain: From interactions to integration. Cambridge MA: MIT Press.

Phelps, E. A. (2004). Human emotion and memory: interactions of the amygdala and hippocampal complex. *Curr. Opin. Neurobiol.* 14, 198–202. doi: 10.1016/j.conb.2004.03.015

Phelps, E. A. (2006). Emotion and cognition: insights from studies of the human amygdala. *Annu. Rev. Psychol.* 57, 27–53. doi: 10.1146/annurev.psych.56.091103.070234

Phelps, E. A., Ling, S., and Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychol. Sci.* 17, 292–299. doi: 10.1111/j.1467-9280.2006.01701.x

Phelps, E. A., and Sharot, T. (2008). How (and why) emotion enhances the subjective sense of recollection. Curr. Dir. Psychol. Sci. 17, 147–152. doi: 10.1111/j.1467-8721.2008.00565.x

Polyn, S. M., Norman, K. A., and Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. Psychol Rev. 116, 129 –156. doi: 10.1037/a0014420

Pourtois, G., Spinelli, L., Seeck, M., and Vuilleumier, P. (2010). Temporal precedence of emotion over attention modulations in the lateral amygdala: intracranial ERP evidence from a patient with temporal lobe epilepsy. *Cogn. Affect. Behav. Neurosci.* 10, 83–93. doi: 10.3758/CABN.10.1.83

Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., et al. (2011). Functional network organization of the human brain. *Neuron* 72, 665–678. doi: 10.1016/j.neuron.2011.09.006

Power, J. D., and Petersen, S. E. (2013). Control-related systems in the human brain. *Curr. Opin. Neurobiol.* 23, 223–228. doi: 10.1016/j.conb.2012.12.009

Price, J. L., and Drevets, W. C. (2009). Neurocircuitry of mood disorders. *Neuropsychopharmacology* 35, 192–216. doi: 10.1038/npp.2009.104

Qin, S., Cousijn, H., Rijpkema, M., Luo, J., Franke, B., Hermans, E. J., et al. (2012). The effect of moderate acute psychological stress on working memory-related neural activity is modulated by a genetic variation in catecholaminergic function in humans. *Front. Integr. Neurosci.* 6:16. doi: 10.3389/fnint.2012.00016

Qin, S., Hermans, E. J., van Marle, H. J., Luo, J., and Fernandez, G. (2009). Acute psychological stress reduces working memory-related activity in the dorsolateral prefrontal cortex. *Biol. Psychiatry* 66, 25–32. doi: 10.1016/j.biopsych.2009.03.006

Ranganath, C., Cohen, M. X., Dam, C., and D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *J. Neurosci.* 24, 3917–3925. doi: 10.1523/JNEUROSCI.5053-03.2004

Rauch, S. L., Shin, L. M., and Phelps, E. A. (2006). Neurocircuitry models of posttraumatic stress disorder and extinction: human neuroimaging research--past, present, and future. *Biol. Psychiatry* 60, 376–382. doi: 10.1016/j.biopsych.2006.06.004

Raymond, J. E., Shapiro, K. L., and Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: an attentional blink? *J. Exp. Psychol. Hum. Percept. Perform.* 18, 849–860. doi: 10.1037/0096-1523.18.3.849

Reisberg, D., and Heuer, F. (2004). Memory for emotional events. In D. Reisberg and P. Hertel (Eds.), Memory and Emotion (pp. 3–41). Oxford University Press. doi: 10.1093/acprof:oso/9780195158564.003.0001

Reisberg, D., and Heuer, F. (2007). "The influence of emotion on memory in forensic settings" in The handbook of eyewitness psychology. Vol. I: Memory for events. eds. M. P. Toglia, D. J. Read, D. F. Ross and R. C. L. Lindsay (Mahwah, NJ: Lawrence Erlbaum Associates, Inc), 81–116.

Riener, C. R., Stefanucci, J. K., Proffitt, D. R., and Clore, G. (2011). An effect of mood on the perception of geographical slant. *Cogn. Emot.* 25, 174–182. doi: 10.1080/02699931003738026

Ritchey, M., Dolcos, F., Eddington, K. M., Strauman, T. J., and Cabeza, R. (2011). Neural correlates of emotional processing in depression: changes with cognitive behavioral therapy and predictors of treatment response. *J. Psychiatr. Res.* 45, 577–587. doi: 10.1016/j.jpsychires.2010.09.007

Roozendaal, B., McEwen, B. S., and Chattarji, S. (2009). Stress, memory and the amygdala. *Nat. Rev. Neurosci.* 10, 423–433. doi: 10.1038/nrn2651

Roozendaal, B., Okuda, S., Van der Zee, E. A., and McGaugh, J. L. (2006). Glucocorticoid enhancement of memory requires arousal-induced noradrenergic activation in the basolateral amygdala. *Proc. Natl. Acad. Sci. USA* 103, 6741–6746. doi: 10.1073/pnas.0601874103

Roozendaal, B., Schelling, G., and McGaugh, J. L. (2008). Corticotropin-releasing factor in the basolateral amygdala enhances memory consolidation via an interaction with the β-adrenoceptor-cAMP pathway: dependence on glucocorticoid receptor activation. *J. Neurosci.* 28, 6642–6651. doi: 10.1523/JNEUROSCI.1336-08.2008

Rottenberg, J., and Gross, J. J. (2003). When emotion Goes wrong: realizing the promise of affective science. *Clin. Psychol. Sci. Pract.* 10, 227–232. doi: 10.1093/clipsy.bpg012

Saal, D., Dong, Y., Bonci, A., and Malenka, R. C. (2003). Drugs of abuse and stress trigger a common synaptic adaptation in dopamine neurons. *Neuron* 37, 577–582. doi: 10.1016/S0896-6273(03)00021-7

Sacher, J., Okon-Singer, H., and Villringer, A. (2013). Evidence from neuroimaging for the role of the menstrual cycle in the interplay of emotion and cognition. *Front. Hum. Neurosci.* 7:374. doi: 10.3389/fnhum.2013.00374

Safer, M. A., Christianson, S. A., Autry, M. W., and Osterlund, K. (1998). Tunnel memory for traumatic events. *Appl. Cogn. Psychol.* 12, 99–117. doi: 10.1002/(SICI)1099-0720(199804)12:2<99::AID-ACP509>3.0.CO;2-7

Sakaki, M., Fryer, K., and Mather, M. (2014a). Emotion strengthens high-priority memory traces but weakens low-priority memory traces. *Psychol. Sci.* 25, 387–395. doi: 10.1177/0956797613504784

Sakaki, M., Ycaza-Herrera, A. E., and Mather, M. (2014b). Association learning for emotional harbinger cues: when do previous emotional associations impair and when do they facilitate subsequent learning of new associations? *Emotion* 14, 115–129. doi: 10.1037/a0034320

Sander, D., Grandjean, D., and Scherer, K. R. (2005). A systems approach to appraisal mechanisms in emotion. *Neural Netw.* 18, 317–352. doi: 10.1016/j.neunet.2005.03.001

Sandi, C., and Pinelo-Nava, M. T. (2007). Stress and memory: behavioral effects and neurobiological mechanisms. *Neural Plast.* 2007:78970. doi: 10.1155/2007/78970

Sara, S. J., and Bouret, S. (2012). Orienting and reorienting: the locus Coeruleus mediates cognition through arousal. *Neuron* 76, 130–141. doi: 10.1016/j.neuron.2012.09.011

Scheuerecker, J., Frodl, T., Koutsouleris, N., Zetzsche, T., Wiesmann, M., Kleemann, A. M., et al. (2007). Cerebral differences in explicit and implicit emotional processing--an fMRI study. *Neuropsychobiology* 56, 32–39. doi: 10.1159/000110726

Schwabe, L., and Wolf, O. T. (2010). Emotional modulation of the attentional blink: is there an effect of stress? *Emotion* 10, 283–288. doi: 10.1037/a0017751

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., et al. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *J. Neurosci.* 27, 2349–2356. doi: 10.1523/jneurosci.5587-06.2007

Shafer, A. T., and Dolcos, F. (2012). Neural correlates of opposing effects of emotional distraction on perception and episodic memory: an event-related fMRI investigation. *Front. Integr. Neurosci.* 6:70. doi: 10.3389/fnint.2012.00070

Shafer, A. T., Matveychuk, D., Penney, T., O'Hare, A. J., Stokes, J., and Dolcos, F. (2012). Processing of emotional distraction is both automatic and modulated by attention: evidence from an event-related fMRI investigation. *J. Cogn. Neurosci.* 24, 1233–1252. doi: 10.1162/jocn_a_00206

Sheline, Y. I., Barch, D. M., Donnelly, J. M., Ollinger, J. M., Snyder, A. Z., and Mintun, M. A. (2001). Increased amygdala response to masked emotional faces in depressed subjects resolves with antidepressant treatment: an fMRI study. *Biol. Psychiatry* 50, 651–658. doi: 10.1016/S0006-3223(01)01263-X

Shin, L. M., and Liberzon, I. (2009). The neurocircuitry of fear, stress, and anxiety disorders. *Neuropsychopharmacology* 35, 169–191. doi: 10.1038/npp.2009.83

Siegel, E. H., and Stefanucci, J. K. (2011). A little bit louder now: negative affect increases perceived loudness. *Emotion* 11, 1006–1011. doi: 10.1037/a0024590

Siegle, G. J., Ingram, R. E., and Matt, G. E. (2002). Affective interference: an explanation for negative attention biases in dysphoria? *Cogn. Ther. Res.* 26, 73–87. doi: 10.1023/A:1013893705009

Siegle, G. J., Thompson, W., Carter, C. S., Steinhauer, S. R., and Thase, M. E. (2007). Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: related and independent features. *Biol. Psychiatry* 61, 198–209. doi: 10.1016/j.biopsych.2006.05.048

Smallwood, J., and Schooler, J. W. (2006). The restless mind. *Psychol. Bull.* 132, 946–958. doi: 10.1037/0033-2909.132.6.946

Staresina, B. P., and Davachi, L. (2010). Object unitization and associative memory formation are supported by distinct brain regions. *J. Neurosci.* 30, 9890–9897. doi: 10.1523/JNEUROSCI.0826-10.2010

Stefanucci, J. K., and Proffitt, D. R. (2009). The roles of altitude and fear in the perception of height. *J. Exp. Psychol. Hum. Percept. Perform.* 35, 424–438. doi: 10.1037/a0013894

Steinmetz, K. R., and Kensinger, E. A. (2013). The emotion-induced memory trade-off: more than an effect of overt attention? *Mem. Cogn.* 41, 69–81. doi: 10.3758/s13421-012-0247-8

St Jacques, P. L., Dolcos, F., and Cabeza, R. (2010). Effects of aging on functional connectivity of the amgydala during negative evaluation: a network analysis of fMRI data. *Neurobiol. Aging* 31, 315–327. doi: 10.1016/j.neurobiolaging.2008.03.012

Sutherland, M. R., and Mather, M. (2012). Negative arousal amplifies the effects of saliency in short-term memory. *Emotion* 12, 1367–1372. doi: 10.1037/a0027860

Sylvester, C. M., Corbetta, M., Raichle, M. E., Rodebaugh, T. L., Schlaggar, B. L., Sheline, Y. I., et al. (2012). Functional network dysfunction in anxiety and anxiety disorders. *Trends Neurosci.* 35, 527–535. doi: 10.1016/j.tins.2012.04.012

Talmi, D., Lohnas, L. J., and Daw, N. D. (2019). A retrieved context model of the emotional modulation of memory. Psychol Rev. 126, 455–485. doi: 10.1037/rev0000132

Talmi, D., and Palombo, D. J. (2024). Emotional time travel: the role of emotion in temporal memory. *Cognit. Emot.* doi: 10.1080/02699931.2024.242139

Tessitore, A., Hariri, A. R., Fera, F., Smith, W. G., Das, S., Weinberger, D. R., et al. (2005). Functional changes in the activity of brain regions underlying emotion processing in the elderly. *Psychiatry Res.* 139, 9–18. doi: 10.1016/j.pscychresns.2005.02.009

Tubridy, S., and Davachi, L. (2011). Medial temporal lobe contributions to episodic sequence encoding. *Cereb. Cortex* 21, 272–280. doi: 10.1093/cercor/bhq092

Uddin, L. Q. (2014). Salience processing and insular cortical function and dysfunction. *Nat. Rev. Neurosci.* 16, 55–61. doi: 10.1038/nrn3857

Vanlessen, N., De Raedt, R., Koster, E. H. W., and Pourtois, G. (2016). Happy heart, smiling eyes: a systematic review of positive mood effects on broadening of visuospatial attention. *Neurosci. Biobehav. Rev.* 68, 816–837. doi: 10.1016/j.neubiorev.2016.07.001

van Marle, H. J., Hermans, E. J., Qin, S., and Fernandez, G. (2009). From specificity to sensitivity: how acute stress affects amygdala processing of biologically salient stimuli. *Biol. Psychiatry* 66, 649–655. doi: 10.1016/j.biopsych.2009.05.014

Ventura-Bort, C., Katsumi, Y., Wirkner, J., Wendt, J., Schwabe, L., Hamm, A., et al. (2024). Disentangling emotional source memory: a mega-analysis on the effects of emotion on item-context binding in episodic long-term memory. Frontiers in psychology – section emotion. *Science* 15:1459617. doi: 10.3389/fpsyg.2024.1459617

Vuilleumier, P., Armony, J. L., Driver, J., and Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nat. Neurosci.* 6, 624–631. doi: 10.1038/nn1057

Wagner, G., Sinsel, E., Sobanski, T., Kohler, S., Marinou, V., Mentzel, H. J., et al. (2006). Cortical inefficiency in patients with unipolar depression: an event-related FMRI study with the Stroop task. *Biol. Psychiatry* 59, 958–965. doi: 10.1016/j.biopsych.2005.10.025

Wang, L., LaBar, K. S., Smoski, M., Rosenthal, M. Z., Dolcos, F., Lynch, T. R., et al. (2008). Prefrontal mechanisms for executive control over emotional distraction are altered in major depression. *Psychiatry Res.* 163, 143–155. doi: 10.1016/j.pscychresns.2007.10.004

Wang, L., Paul, N., Stanton, S. J., Greeson, J. M., and Smoski, M. (2013). Loss of sustained activity in the ventromedial prefrontal cortex in response to repeated stress in individuals with early-life emotional abuse: implications for depression vulnerability. *Front. Psychol.* 4:320. doi: 10.3389/fpsyg.2013.00320

Wang, M., Ramos, B. P., Paspalas, C. D., Shu, Y., Simen, A., Duque, A., et al. (2007). α2A-adrenoceptors strengthen working memory networks by inhibiting cAMP-HCN channel signaling in prefrontal cortex. *Cell* 129, 397–410. doi: 10.1016/j.cell.2007.03.015

Waring, J. D., and Kensinger, E. A. (2009). Effects of emotional valence and arousal upon memory trade-offs with aging. *Psychol. Aging* 24, 412–422. doi: 10.1037/a0015526

Waring, J. D., Payne, J. D., Schacter, D. L., and Kensinger, E. A. (2010). Impact of individual differences upon emotion-induced memory trade-offs. *Cogn. Emot.* 24, 150–167. doi: 10.1080/02699930802618918

Watson, D. (2000). Mood and temperament. New York, NY: Guilford Press.

Whitmer, A. J., and Gotlib, I. H. (2013). An attentional scope model of rumination. *Psychol. Bull.* 139, 1036–1061. doi: 10.1037/a0030923

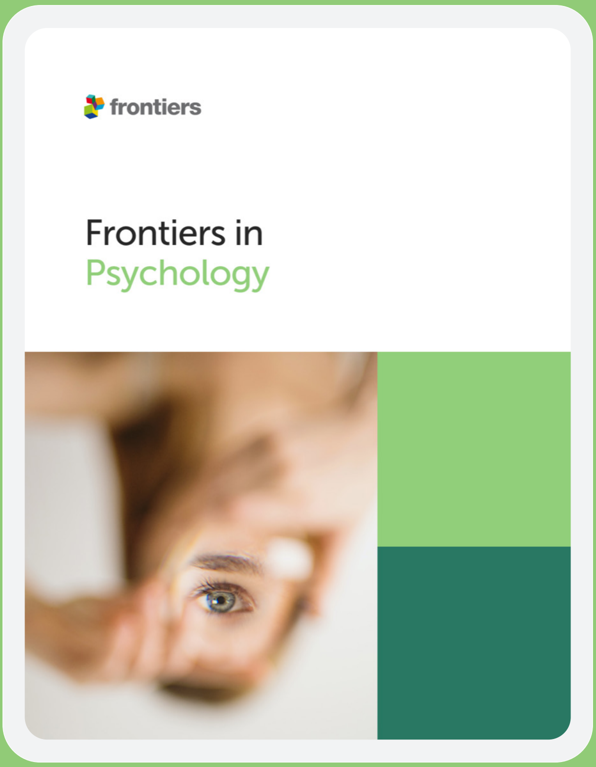
Wood, S., and Kisley, M. A. (2006). The negativity bias is eliminated in older adults: age-related reduction in event-related brain potentials associated with evaluative categorization. *Psychol. Aging* 21, 815–820. doi: 10.1037/0882-7974.21.4.815

Yeo, B. T., Krienen, F., Sepulcre, J., Sabuncu, M., Lashkari, D., Hollinshead, M., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* 106, 1125–1165. doi: 10.1152/jn.00338.2011

Yonelinas, A. P., and Ritchey, M. (2015). The slow forgetting of emotional episodic memories: an emotional binding account. *Trends Cogn. Sci.* 19, 259–267. doi: 10.1016/j.tics.2015.02.009

Yuen, E. Y., Liu, W., Karatsoreos, I. N., Ren, Y., Feng, J., McEwen, B. S., et al. (2011). Mechanisms for acute stress-induced enhancement of glutamatergic transmission and working memory. *Mol. Psychiatry* 16, 156–170. doi: 10.1038/mp.2010.50

Zadra, J. R., and Clore, G. L. (2011). Emotion and perception: the role of affective information. *Wiley Interdiscip. Rev. Cogn. Sci.* 2, 676–685. doi: 10.1002/wcs.147



Frontiers

Avenue du Tribunal-Fédéral 34
1005 Lausanne, Switzerland
frontiersin.org

Contact us

+41 (0)21 510 17 00
frontiersin.org/about/contact