Institute of Psychology
Polish Academy of Sciences

Graduate School for Social Research
Institute of Psychology, Polish Academy of Sciences

Neural and Parasympathetic Mechanisms of Momentary and Chronic Loneliness During Social Information Processing

[Neuronalne i przywspółczulne mechanizmy chwilowej i chronicznej samotności podczas przetwarzania informacji społecznych]

Mgr Marcelina Wiśniewska

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Dr hab. Łukasz Okruszek, prof. IP PAN

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Abstract

Loneliness, defined as subjective, distressing feelings of one's relationships not being sufficient in relation to their social needs, has been associated with deleterious health outcomes. One of the most prominent theories, proposed to explain the mechanisms linking psychophysiological mechanisms observed in loneliness to short- and long-term consequences, is the Evolutionary Theory of Loneliness (ETL). According to the ETL, loneliness is associated with increased bottom-up social threat perception, which in turn might impact top-down processing of social information. Therefore, the investigations regarding neural correlates of loneliness have focused on functioning of the brain structures associated with threat perception (amygdala; AMY), and mentalizing (the medial prefrontal cortex; mPFC, the temporoparietal junction; TPJ). Associations between these structures are also essential for adaptive responding to environmental demands, as posited by the Neurovisceral Integration Model (NIM). Importantly, the NIM emphasizes the role of heart rate variability (HRV) as a marker of context-sensitive responding, hence providing a framework for integrating neural and parasympathetic responses, and examining their associations in relation to loneliness.

The available results of the studies regarding cognitive mechanisms associated with loneliness are predominantly based on the cross-sectional investigations of participants characterized by the high and low levels of chronic loneliness. However, the examination of the impact of momentary loneliness on physiological responses might further extend the understanding of the trajectories underlying mechanisms observed in chronically lonely individuals. Therefore, this dissertation aimed at investigating parasympathetic and neural responses to social information in relation to momentary and chronic loneliness. Consequently, three studies were conducted. The first two studies used an experimental manipulation to investigate causal influence of momentary loneliness on parasympathetic (study 1 and 2) and neural (study 2) correlates of social information processing. In turn, the third study aimed at examining associations between parasympathetic and neural responses to social information, and chronic loneliness. We hypothesized that momentary and chronic loneliness will be linked to 1) increased negative affect and decreased positive affect, 2) decreased vagal flexibility, as indicated by the HRV task-related changes, which in turn will be associated with 3) decreased social brain activity. Furthermore, we expected to observe decreased task-related connectivity between the social brain structures and the AMY in chronically lonely compared to non-lonely participants.

In the first study, 128 individuals were randomly assigned to either future alone (FA) or future belong (FB) condition, and were asked to complete a social information processing task, while their changes in HRV were measured. In the second study, 63 participants were subjected to a corresponding experimental manipulation procedure during a neuroimaging session while their parasympathetic and neural responses to a social information processing task were recorded. The third study included 104 individuals with either high- or low-levels of chronic loneliness who completed a social information processing task while their neural and cardiac responses were measured. Additionally, in each of the studies, affect ratings were collected during the procedure.

Across all three presented studies, we observed hypothesized differences in affect ratings during the corresponding procedures. Additionally, in both studies which utilized the induction of loneliness, a decreased pattern of vagal flexibility was observed in the FA in comparison to the FB group, which might indicate reduced task mobilization as the result of momentary loneliness. While no significant between-group differences in activation of the main regions linked to the 'social brain' were found, a positive correlation was observed between vagal flexibility and the left TPJ activation in the second study, which may suggest a need for compensatory processing of socioaffective information as the result of momentary loneliness. Despite the absence of the hypothesized findings, we observed tentative evidence for differences between lonely and non-lonely individuals in the processing of social information at early stages of the visual pathway in the exploratory analysis.

Taken together, the presented results were only partly congruent with the hypotheses. Thus, this work emphasizes that mechanisms accompanying momentary loneliness do not extend to chronic loneliness. As these findings do not support the psychophysiological mechanisms suggested by the ETL, a different conceptualization for investigating mechanisms underlying loneliness might be required.

Keywords: functional magnetic resonance imaging, heart rate variability, loneliness, social information processing

Streszczenie

Jak wskazują badania, samotność, definiowana jako subiektywne, nieprzyjemne odczucie wywołane rozbieżnością między ilością lub jakością posiadanych związków a czyimiś potrzebami społecznymi, wiąże się z licznymi szkodliwymi skutkami zdrowotnymi. Jedną z wiodących teorii, które zaproponowane zostały w celu wyjaśnienia psychofizjologicznych mechanizmów obserwowanych w nawiązaniu do krótko- i długotrwałych konsekwencji samotności, jest Ewolucyjna Teoria Samotności (ETS). Zgodnie z ETS, u osób samotnych obserwować można zwiększoną aktywność automatycznych procesów związanych z postrzeganiem zagrożeń społecznych, co może negatywnie wpływać również na przetwarzanie informacji społecznych na poziomie mechanizmów wolicjonalnych. Z tego powodu badania dotyczące neuronalnych korelatów samotności skupiały się dotychcazs na funkcjonowaniu struktur mózgu związanych z percepcją zagrożeń (ciało migdałowate, ang. *amygdala*; AMY) oraz atrybucją intencji (przyśrodkowa kora przedczołowa, ang. *medial prefrontal cortex*; mPFC i styk skroniowo-ciemieniowy, ang. *temporoparietal junction*; TPJ). Dodatkowo, jak wskazuje Model Integracji Neurowisceralnej (ang. *Neurovisceral Integration Model*, NIM), interakcje między wymienionymi strukturami mózgowymi są także istotne dla sprawnego reagowania na wymagania środowiska. Jak wskazuje NIM, z uwagi na połączenia funkcjonalne między układem nerwowym i sercowo-naczyniowym, zmienność rytmu serca (ang. *heart rate variability*, HRV) stanowić może wskaźnik zdolności odpowiedzi na potencjalne zagrożenia ze środowiska. Model ten oferuje ramę pojęciową pozwalającą na integrację reakcji neuronalnych i przywspółczulnych, a także badanie ich współzależności w kontekście samotności.

Dostępne wyniki badań dotyczące mechanizmów poznawczych związanych z samotnością w dużej mierze opierają się na badaniach osób charakteryzujących się wysokim i niskim nasileniem chronicznej samotności. Zbadanie wpływu chwilowej samotności na odpowiedzi fizjologiczne mogłoby rozszerzyć rozumienie trajektorii zmian obserwowanych u osób chronicznie samotnych. Celem niniejszej rozprawy, obejmującej trzy badania, było zbadanie reakcji przywspółczulnych i neuronalnych obserwowanych w odpowiedzi na informacje społeczne w odniesieniu zarówno do chwilowej, jak i chronicznej samotności. Pierwsze dwa badania opierały się na procedurze mającej na celu sprawdzenie, jak eksperymentalna indukcja poczucia samotności wpływa na aktywność przywspółczulną (badania 1 i 2) i neuronalną (badanie 2) obserwowaną podczas przetwarzania bodźców społecznych. Z kolei trzecie badanie miało na celu ustalenie,

czy istnieje związek pomiędzy wskaźnikami przywspółczulnymi i neuronalnymi obserwowanymi podczas przetwarzania informacji społecznych a chroniczną samotnością. Przewidywano, że zarówno chwilowa jak i chroniczna samotność będą związane ze 1) zwiększonym poziomem negatywnego i zmniejszonym poziomem pozytywnego afektu, 2) zmniejszeniem elastyczności odpowiedzi nerwu błędnego, określonej jako zmiany HRV podczas zadania, która z kolei będzie związana ze 3) zmniejszoną aktywnością obszarów tzw. mózgu społecznego. Ponadto spodziewano się zaobserwować związaną z zadaniem zmniejszoną łączność funkcjonalną pomiędzy regionami mózgu społecznego a AMY u osób chronicznie samotnych w porównaniu do osób niesamotnych.

W pierwszym badaniu 128 uczestników zostało przydzielonych w sposób losowy do jednego z dwóch warunków eksperymentalnych: indukcja poczucia samotności (ang. *future alone*, FA) lub przynależności (ang. *future belong*, FB). Następnie uczestników poproszono o wykonanie zadania dotyczącego przetwarzania informacji społecznych w trakcie rejestracji aktywności sercowo-naczyniowej. W drugim badaniu analogicznej procedurze poddano 63 uczestników, tym razem jednak obok aktywności sercowo-naczyniowej w ramach sesji neuroobrazowania rejestrowano również aktywność mózgu. W ramach trzeciego badania wzorce odpowiedzi neuronalnej i sercowo-naczyniowej na bodźce społeczne i niespołeczne porównano pomiędzy grupami 52 osób o wysokim i 52 osób o niskim nasileniu chronicznego poczucia samotności. Podczas każdego z badań zbierano oceny dotyczące odczuwanego afektu.

W każdym z trzech badań zaobserwowaliśmy przewidywane różnice pomiędzy grupami w nasileniu pozytywnego i negatywnego afektu. Dodatkowo, w obu badaniach eksperymentalnych zaobserwowano wzorzec obniżonej elastyczności odpowiedzi nerwu błędnego w grupie FA w porównaniu do grupy FB, co może wskazywać, że chwilowe poczucie samotności obniża mobilizację zasobów fizjologicznych do wykonania zadania. Mimo że nie wykazano istotnych różnic pomiędzy grupami w aktywności głównych regionów „mózgu społecznego", w badaniu eksperymentalnym zaobserwowano pozytywny związek pomiędzy elastycznością odpowiedzi nerwu błędnego a lewym TPJ, co stanowić może potencjalny mechanizm kompensacyjny związany z indukcją chwilowego poczucia samotności. Dodatkowo, w ramach analizy eksploracyjnej danych z badania porównawczego zaobserwowaliśmy różnice pomiędzy osobami samotnymi i niesamotnymi w zakresie wzorców wczesnego przetwarzania bodźców społecznych.

Podsumowując, przedstawione wyniki jedynie częściowo pokrywają się z postawionymi hipotezami. Przeprowadzone w ramach rozprawy badania dostarczają

dowodów, że mechanizmy związane z chwilową samotnością nie przekładają się na efekty obserwowane w grupie osób chronicznie samotnych. Z uwagi na to, że wyniki nie wspierają psychofizjologicznych mechanizmów sugerowanych przez ETS, potrzebna jest dalsza rekonceptualizacja mechanizmów leżących u podstaw samotności.

Słowa kluczowe: funkcjonalny rezonans magnetyczny, zmienność rytmu serca, samotność, przetwarzanie informacji społecznych

Introduction

Loneliness may be defined as a subjective, distressing feeling that emerges when the quality and quantity of an individual's achieved relationships are perceived as insufficient in relation to their social needs (Perlman & Peplau, 1981). Importantly, loneliness, also referred to as perceived social isolation, has been demonstrated to only weakly correlate to objective social isolation, defined as objective lack of social interactions and relationships (Coyle & Dugan, 2012). The high prevalence of loneliness (Beutel et al., 2017) and associations between prolonged feelings of loneliness and negative mental and physical health sequelae (C. Park et al., 2020) highlight the importance of addressing loneliness when considering overall health and well-being. Consequently, chronic loneliness has been considered a risk factor for all-cause mortality (Holt-Lunstad et al., 2015), and has been linked to higher risk of cardiovascular disease (Paul et al., 2021; Vasan et al., 2024), developing dementia (Dabiri et al., 2024), and a higher prevalence of depressive symptoms (Z. Chen et al., 2023) and anxiety (Lim et al., 2016). Although loneliness has been demonstrated to often accompany mental disorders (Nuyen et al., 2020), or situational social isolation (Ernst et al., 2022), it may also emerge without objective conditions as a momentary state, or be considered a trait–like characteristic. Given the severe consequences of loneliness, it is crucial to understand the underlying psychophysiological mechanisms and examine whether these underpinnings are distinct for momentary and chronic experience of loneliness.

Evolutionary Theory of Loneliness

One of the most prominent theories which attempts to pinpoint mechanisms through which loneliness affects everyday social functioning and negatively impacts health outcomes is the Evolutionary Theory of Loneliness (ETL; Cacioppo & Cacioppo, 2018). From an evolutionary perspective, reliable social relationships were necessary to enhance the likelihood of survival, as being part of a group facilitated acquisition of resources or protection against predators. Therefore, according to the ETL, social relationships play a beneficial role in human survival. Consequently, as it is posited by the ETL, if an unmet need for social belonging occurs, it serves as a signal that motivates an individual to repair or replace their social relationships in order to reconnect with others. Loneliness should thus, according to the ETL, strengthen the motivation to approach others. However, as it also increases focus on self-preservation and avoidance of potential threats, it may activate cognitive mechanisms leading to abnormal social information processing. Accordingly, the ETL posits that mechanisms initiated to ensure short-term survival affect responses to everyday interactions with others, and might lead to hypervigilance to social threats in lonely individuals (Cacioppo & Hawkley, 2009). Furthermore, the ETL posits that the long-term effects of mechanisms activated for self-preservation purposes might result in the cascade of the cognitive and behavioral alterations leading to increased social disconnection, and detrimental health and well-being consequences. Thus, the ETL provides a framework for investigating loneliness and its underlying mechanisms which impact momentary impressions of loneliness and which are consolidated in chronically lonely individuals.

Integrating psychological and physiological correlates of loneliness

The ETL provides insights into mechanisms linking loneliness to maladaptive cognitive patterns that may contribute to further outcomes. However, it does not completely disentangle how psychological and physiological dimensions interact to result in severe consequences associated with loneliness. As loneliness is a subjective psychological phenomenon, understanding how its links to negative health effects arise may encompass alterations in functioning of central (CNS) and peripheral (PNS) nervous systems. The autonomic nervous system, as part of the PNS, consists of sympathetic and parasympathetic branches which regulate involuntary physiological processes. Hence, ineffective physiological regulation may provide a plausible mechanism by which loneliness results in negative health outcomes. As this section focuses on general psychophysiological mechanisms in association with loneliness, findings regarding CNS and PNS functioning with regard to momentary and chronic loneliness are presented in the subsequent sections.

A large body of research emphasized alternations of functioning of the sympathetic nervous system in relation to loneliness (Brown et al., 2018), particularly, increased inflammatory reactions (Jaremka et al., 2013; Matthews et al., 2024), and hypothalamic-pituitary adrenocortical axis reactivity linked to alterations in levels of cortisol patterns (Nowland et al., 2018). Similarly, the association between loneliness and the functioning of the parasympathetic nervous system has also been investigated, with a particular focus on changes in heart rate variability (HRV) which reflects the influence of the vagus nerve on cardiac functioning (Laborde et al., 2017). One theory that might provide a framework for understanding trajectories linking psychological and physiological mechanisms associated with loneliness is the Neurovisceral Integration Model, which focuses on HRV to combine central and autonomic nervous system functioning (NIM; Thayer & Lane, 2000). In line with the NIM, HRV is influenced by subcortical and prefrontal circuits through the nucleus of the solitary tract located in the brainstem (Smith et al., 2017; Thayer & Lane, 2000). Thus, HRV might serve as a marker of brain mechanisms that guide flexible responding in a changing environment and provide insights into physical and mental health (Thayer et al., 2009).

In particular, the NIM emphasizes the role of interplay between the amygdala (AMY) and the medial prefrontal cortex (mPFC) for affective regulation. The AMY is a subcortical structure with a well-defined role in automatic emotional processing (Sergerie et al., 2008), including threat processing (De Gelder et al., 2014). In turn, the mPFC is a cortical region with a role in higher cognitive processes, such as understanding perspective of others (Molenberghs et al., 2016) and modulation of reactivity to stimuli based on available contextual information (Lee & Siegle, 2014). Therefore, if the top-down cortical control over the AMY responses is inefficient, it may result in increased threat responding (Thayer et al., 2012). Consequently, as HRV has been associated with the mPFC-AMY interaction (Sakaki et al., 2016; Wei et al., 2018), it could potentially link physiological mechanisms underlying loneliness to social threat hypervigilance postulated by the ETL. The NIM focuses on the prefrontal regions' inhibitory mechanisms in relation to HRV (Smith et al., 2017), however, a regulatory role over subcortical structures has also been attributed to the temporoparietal junction (TPJ; Y. Cheng et al., 2022). The role of the TPJ has been highlighted in perspective-taking (Molenberghs et al., 2016), as well as in attentional processes with the role of the right TPJ in orienting to salient stimuli (Mavritsaki et al., 2010), and the left TPJ in semantic information processing and integration (He et al., 2025). Moreover, the function of the TPJ in the integration of neural response and HRV has been demonstrated in resting-state data (Chang et al., 2013), and through modulating psychophysiological responding during emotion-induction task (Miller et al., 2020). Thus, the TPJ might also contribute to neurovisceral regulation and understanding of interactions between neural and physiological responses in relation to loneliness.

Moreover, HRV measured at rest, also termed vagal tone, has been considered an important predictor of health, with lower vagal tone being linked to all-cause and cardiac mortality (Jarczok et al., 2022), inflammation (D. P. Williams et al., 2019), depression severity (Kemp et al., 2010), and anxiety disorders (Y.-C. Cheng et al., 2022). Hence, the inclusion of HRV in the investigation of mechanisms underlying momentary and chronic experience of loneliness could extend the understanding of how health problems observed in relation to loneliness emerge and might be consolidated. Additionally, higher vagal tone has also been observed to reflect the efficiency of cognitive functioning, involving attentional control (G. Park et al., 2014), inhibitory processes (Magnon et al., 2022), emotion processing (Schmaußer & Laborde, 2023) and emotion regulation (Balzarotti et al., 2017). Taking into consideration previous evidence demonstrating poorer cognitive functioning of lonelier individuals (Yin et al., 2019), it may further connect loneliness to its underlying biological mechanisms. Similarly, vagal flexibility, defined as dynamic change between HRV measured at rest and during attentional or cognitive demand (Muhtadie et al., 2015), presents an adaptive pattern of physiological responding. Hence, greater values of vagal flexibility indicate higher cognitive effort to task-specific demands (G. Park et al., 2014; Spangler & McGinley, 2020), and might be indicative of task engagement in association with both momentary and chronic loneliness. Furthermore, in the study by Muhtadie et al., (2015), greater vagal flexibility was associated with lower levels of loneliness, which might also exemplify physiological mechanisms linked to decreased sensitivity to social context in lonely individuals.

Momentary loneliness

Momentary loneliness is a common human experience, which frequency and intensity may vary depending on everyday events and social interactions. According to the ETL, loneliness can be experienced as a transient state that should motivate an individual to improve their social connections (Qualter et al., 2015), but may actually initiate a cascade of processes which may deepen social withdrawal due to heightened social threat perception (Hawkley & Cacioppo, 2010). The use of experience sampling method (ESM) has allowed to demonstrate that momentary loneliness is associated with increased negative affect (Meng et al., 2020), negative perception of others and solitary situations (Piejka et al., 2024), and with increased depressed mood (Kuczynski et al., 2024). At the same time, while ESM methodology can be used to investigate how transient loneliness is linked to real-life situations, it does not allow for establishing causality between loneliness and its correlates. To address this issue, studies experimentally induce momentary loneliness in the laboratory settings to examine behavioral and physiological responses. There are various methods of experimental loneliness induction used by the researchers in the field, such as asking participants to recall a prior experience of loneliness (Pels & Kleinert, 2017), which has been demonstrated to negatively impact engagement in social situations (Arpin & Mohr, 2019). However, as noted by Wirth et al. (2016) while reviewing paradigms which may be utilized for social exclusion and isolation experiments, the method considered to be the most efficient in evoking a transient state of loneliness is the “Future Life Alone” (Twenge et al., 2001). As part of the Future Alone paradigm, participants receive bogus feedback stating that they will end up alone later in life, aimed at evoking an unpleasant sense of lacking in social relationships. In contrast, other participants obtain information that they will have a fulfilling social life in the future, evoking feelings of belonging (Future Belong condition). Accordingly, loneliness induced with the Future Alone paradigm has been demonstrated to negatively affect self-regulation (Baumeister et al., 2005), reduce prosocial behavior (Twenge et al., 2007), and to lead to self-defeating behavior (Twenge et al., 2002) and emotional insensitivity (DeWall & Baumeister, 2006). These results demonstrate that even transient feelings of anticipated loneliness might negatively impact social functioning (Wirth, 2016). Therefore, it is possible to investigate how momentary loneliness affects cognitive and physiological processes, which may enable us to determine whether the effects of loneliness result from long-term changes that emerge when loneliness becomes chronic.

Notably, the experimental manipulation via Future Alone paradigm has been shown to impact neural response to social information, specifically, by reducing activation of the dorsomedial prefrontal cortex (dmPFC) to negative social content (Powers et al., 2013). As the dmPFC is a region largely associated with mentalizing, its decreased recruitment could thus potentially link loneliness to worse understanding of social cues and disengagement from negative aspects of social interactions (Powers et al., 2013). Other methods aimed to induce momentary loneliness have also demonstrated its deleterious effects on parasympathetic regulation (Roddick and Chen 2021). Finally, following a manipulation based on subjecting participants to acute social isolation, a selective responsiveness of the midbrain regions to social cues has also been observed (Tomova et al., 2020). As a similar neural response was observed to food cues after fasting under comparable experimental conditions, it was suggested that short-term social isolation might result in social cravings motivating an individual to focus on social connections (Tomova et al., 2020). These findings indicate that even transient feelings of loneliness may impact parasympathetic and neural responses. However, these responses have not yet been examined concurrently to better understand how the momentary loneliness induction impacts coupling between central and peripheral nervous system.

Chronic loneliness

While the cognitive mechanisms associated with prolonged experience of loneliness have been examined more thoroughly than the effects of momentary loneliness, the investigation of the link between chronic loneliness and social cognition abilities has produced mixed findings. Studies demonstrated evidence for an association between loneliness and less efficient social cognition (Kanai et al., 2012; Smogorzewska et al., 2024), better performance depending on task conditions (Di Tella et al., 2023; Vanhalst et al., 2017), or a non-significant relationship (De Lillo et al., 2023; Lodder et al., 2016). It has been further demonstrated that performance in social cognitive tasks encompassing processing of social cues predicted objective social isolation, but not loneliness (Okruszek et al., 2021). At the same time, both loneliness and objective social isolation were predicted by hostile attribution bias, suggesting that proneness to negative subjective attributions made in response to social situations, rather than decreased objective capacity to process social cues, is associated with more pronounced chronic loneliness (Okruszek et al., 2021).

Similarly, the findings regarding associations between chronic loneliness, vagal tone, and vagal flexibility are still inconclusive. A few studies indicated the relationship between loneliness and decreased vagal flexibility (Muhtadie et al., 2015; Roddick and Chen 2021; Song et al., 2025), which may reflect insufficient mobilization towards context-specific task demands in lonelier individuals. Additionally, other studies reported a link between chronic loneliness and lower vagal tone (Gouin et al., 2015; Roddick & Chen, 2021), or no links between them (Hawkley et al., 2006; Muhtadie et al., 2015).

Neural mechanisms associated with chronic loneliness have been studied primarily within the ‘social brain’ network, which includes regions that play crucial roles in social cognitive processes (Adolphs, 2009). Hence, in the context of loneliness, abnormal function and structure of the ‘social brain’ regions, as well as altered connectivity patterns with other areas of the brain, might underlie problems in social cognition and hinder successful social interactions. Furthermore, it has been demonstrated that loneliness scores can be predicted from resting-state (Feng et al., 2019), and social cognitive task-related (Geng et al., 2025) connectivity patterns that encompass regions of the prefrontal cortex, temporal regions, with the TPJ as an essential node, and the limbic system, including the AMY.

Several findings emphasized structural (Ehlers et al., 2017; Nakagawa et al., 2015) and functional (Cacioppo et al., 2009; Courtney & Meyer, 2020) alterations observed in the regions associated with the mentalizing network - namely, the mPFC and the TPJ - in relation to loneliness. Specifically, as decreased activation of the TPJ to negative social stimuli was observed in lonelier individuals, it was suggested that loneliness is associated with limited ability to take the perspective of others (Cacioppo et al., 2009). Moreover, in the same study, lonely (in comparison to non-lonely) participants showed greater dmPFC activation in response to positive non-social stimuli than to social stimuli, which may reflect a tendency to distance oneself from positive social context (Cacioppo et al., 2009). While the findings of Cacioppo et al. (2009) indicate links between loneliness and blunted processing of social content, it is important to note that the conclusions were drawn based on a relatively small sample (n=23) and similar patterns of activations were not replicated in a larger-scale study (n=99) following a similar methodology (D'Agostino et al., 2019).

In line with the ETL's postulate of social threat hypervigilance, chronic loneliness should also be linked to the AMY abnormal functioning. While smaller gray matter volume of the AMY in older adults, who reported being lonelier, has been previously observed (Düzel et al., 2019), studies failed to find association between chronic loneliness and the AMY activation in response to social in comparison to non-social content (D'Agostino et al., 2019; Wong et al., 2016). At the same time, the AMY is believed to constitute a crucial node in several brain networks which may support various social cognitive mechanisms (Bickart et al., 2012). This way, abnormal AMY connectivity rather than the task-related response *per se* may be linked to chronic loneliness. In line with this notion, causal interaction from the affective network, involving the AMY, to the visual network, including the fusiform gyrus and cuneus, has been found to be negatively associated with loneliness in lonelier individuals (Tian et al., 2017). Moreover, in lonelier individuals, decreased resting-state functional connectivity between the AMY and the frontal regions were observed (Layden et al., 2017), which may be reflective of ineffective cortical control over the AMY and link these findings to mechanisms postulated by the NIM.

Research goals and hypotheses

In previous investigations of parasympathetic and neural mechanisms associated with loneliness, emphasis has been put on the chronic experience of loneliness by comparing two groups with distinguishable levels of reported loneliness. As it enables to extend the knowledge of processes in relation to loneliness, at the same time, it does not allow examining causal impact of short-term loneliness. Therefore, this dissertation encompasses four main research questions which were formulated to investigate if the patterns of parasympathetic and neural responses to social information associated with chronic loneliness differ from the patterns observed as the result of momentary loneliness.

Research Question 1: How does momentary loneliness affect behavioral and autonomic responses to social information?

In order to investigate the effects of momentary loneliness on social information processing, experimental manipulation was used. We hypothesized that the induction of loneliness will increase negative affect and decrease positive affect (**H1a**). Based on prior evidence linking loneliness to altered functioning of the autonomic nervous system, we also anticipated that the induction of loneliness will decrease vagal flexibility (**H1b**), and increase sympathetic activity (**H1c**) during social information processing.

Research Question 2: How does momentary loneliness affect coupling between brain activity and parasympathetic responses during social information processing?

Building on the mechanisms posited by the ETL and prior findings from the literature, we hypothesized that the induction of loneliness will increase the activity of regions associated with bottom-up threat responding (**H2a**), and decrease activity of brain regions associated with top-down mentalizing (**H2b**) during social information processing. Moreover, considering the mechanisms postulated by the NIM, we expected to observe that decreased vagal flexibility found in individuals subjected to experimental induction of loneliness will be associated with decreased social brain activity (**H2c**).

Research Question 3: What are the associations between chronic loneliness and behavioral and autonomic responses to social information?

We hypothesized that a higher level of negative affect and a lower level of positive affect will be observed in the chronically lonely compared to non-lonely individuals (**H3a**). While previous investigations provided inconclusive findings regarding the relationship between loneliness and HRV reactivity, in line with the prevalent majority of the findings we also expected to observe decreased vagal flexibility during social information processing in lonely compared to non-lonely individuals (**H3b**).

Research Question 4: What are the associations between chronic loneliness and coupling between brain activity and parasympathetic responses during social information processing?

In line with previous results in existing literature, we anticipated that reduced activity of social brain regions, including the mPFC and the TPJ (**H4a**), and reduced functional connectivity between the social brain regions and the AMY (**H4b**) will be observed in the chronically lonely compared to non-lonely individuals during social information processing. In line with the NIM, we hypothesized that decreased vagal flexibility will be associated with decreased social brain activity in the chronically lonely compared to non-lonely individuals (**H4c**).

Methods and Results

Loneliness is particularly prevalent in young adults (Shovestul et al., 2020), and negative consequences of loneliness, including mental health problems, have been emphasized in this age group (Matthews et al., 2019). Therefore, in each of three studies comprising this dissertation, individuals aged 18-35 were invited. Loneliness was measured with Revised UCLA Loneliness Scale (R-UCLA; Kwiatkowska et al., 2017). In each of the studies, exclusion criteria included history of psychiatric or neurological disorders, substance abuse, cardiovascular diseases, body mass index > 30, and MRI contraindications (in study 2 and 3). Moreover, participants with increased depressive symptomatology (dysphoria score ≥ 12 and anhedonia score ≥ 8), as measured by the Polish version of the revised Center for Epidemiologic Studies Depression Scale (Koziara, 2016), were excluded.

The Ethical Committee at the Institute of Psychology, Polish Academy of Sciences approved protocols for each of the studies (application numbers: 20/XI/2019 and 21/XI/2019). Each behavioral session took place at Institute of Psychology, Polish Academy of Sciences (Warsaw, Poland), while for the neuroimaging session participants were invited to the Bioimaging Research Center of the Institute of Physiology and Pathology of Hearing (Kajetany, Poland). A summary of each publication included in this thesis is provided below. The detailed descriptions of methods and results are presented in each of the three articles appended to the dissertation.

Study 1: Effects of the loneliness induction on the sympathetic and parasympathetic responses

Piejka, A.*, **Wiśniewska, M.***, Thayer, J. F., & Okruszek, Ł. (2021). Brief induction of loneliness decreases vagal regulation during social information processing. *International Journal of Psychophysiology*, *164*, 112-120. https://doi.org/10.1016/j.ijpsycho.2021.03.002

* joint first authorship

The first study was a pilot study of the NCN project OPUS 2018/31/B/HS6/02848 and aimed to investigate the effects of the experimental induction of loneliness on the affective, sympathetic and parasympathetic responses. Taking into account previous correlational evidence demonstrating associations between loneliness and the functions of the sympathetic (Brown et al., 2018) and parasympathetic (Muhtadie et al., 2015) nervous system, the study attempted to investigate the causal role of momentary loneliness, induced in a laboratory setting, on the changes in HRV and stress reactivity. We hypothesized that participants subjected to the loneliness induction, in comparison to the participants in the social belonging condition, would demonstrate reduced vagal flexibility (H1b) during a social information processing task and an increased stress response (H1c) to negative social content. We also expected to observe a higher level of negative affect and a lower level of positive affect as the result of the loneliness induction (H1a).

Methods: The sample consisted of 128 individuals (75F) who were invited to participate in a two-session study. During the first session, the participants completed a set of social cognitive tasks and questionnaires and were informed that based on the results, they will be given feedback regarding their social functioning during the subsequent session. The main experimental procedure designed after Twenge et al. (2001), aimed at inducing either feelings of loneliness, or belonging, took place during the second session. The participants received feedback regarding their extraversion level based on their Eysenck Personality Questionnaire (Jaworowska, 2012) score and then were randomly given either Future Belong (FB; n=62) or Future Alone (FA; n=66) feedback. Participants in the FB condition were told that they will have many fulfilling social connections in the future, while participants in the FA condition were informed that their relationships will not last, and they might end up alone later in life. After receiving the feedback, the participants were asked to complete an implicit emotion regulation task by rating neutral and angry faces and to either increase or decrease their affective response to angry faces during the subsequent phases of the task. During the session, cardiovascular activity and skin conductance level (SCL) data were collected, including pre-feedback and post-task 6-minute resting measures. The participants were asked to provide their self-report affect ratings (e.g. feeling sad, anxious, lonely, relaxed, cheerful) before the experimental manipulation, right after it, and after completing the task. To investigate changes of HRV and SCL during the procedure, high-frequency HRV (HF-HRV; 0.15 – 0.40 Hz) and tonic SCL values respectively, were obtained for each condition, and analyzed with repeated-measures ANOVAs.

Results: Significant changes in affect ratings were observed during the procedure, with a lower level of positive affect and a higher level of negative affect post-manipulation in the FA group, and a reverse pattern observed in the FB group. Significant interaction between Condition and Group was found for HF-HRV changes during the procedure, with significantly higher HRV during baseline and recovery than during all task-related conditions observed in the FB group, while in the FA group a significant change was found only between baseline and the first task-related condition. Moreover, the analysis repeated on the subset of participants who rated the obtained FA/FB feedback as accurate (ratings above four on a seven-point scale; n=91) revealed the same pattern of HRV changes in the FB group, and the lack of initial decrease in HRV from rest to first task condition in the FA group. No effect of Group or an interaction between Condition and Group were found for changes in SCL during the procedure.

Discussion: The effects of experimental manipulation were evident in differences in between-group affective ratings, with increased negative and decreased positive affect observed in the FA in comparison to the FB group. Moreover, the pattern of parasympathetic response indicating task mobilization was evident only in participants in the FB condition. Therefore, the results of the study suggest that an experimental induction of loneliness affected vagal flexibility during social information processing. Conversely, the experimental manipulation did not affect the sympathetic response to social content, which may accentuate the specificity of the impact of momentary loneliness on parasympathetic responding.

Study 2: Effects of the loneliness induction on the parasympathetic and neural responses

Wiśniewska, M., Piejka, A., Wolak, T., Scheele, D., & Okruszek, Ł. (2025). Loneliness-not for the faint of heart? Effects of transient loneliness induction on neural and parasympathetic responses to affective stimuli. *Social Neuroscience*, 1-14. https://doi.org/10.1080/17470919.2025.2498384

The second study aimed to extend the results of the impact of loneliness induction observed in the first study by utilizing the same experimental manipulation procedure and examining its effects on the neural response. As loneliness has been previously linked to altered functioning and structure of several regions associated with the social brain network, we hypothesized increased reactivity of the AMY (H2a) and decreased activation of structures associated with mentalizing (mPFC/TPJ; H2b) during social information processing as a response to momentary loneliness. Moreover, based on the mechanisms proposed by the NIM, we expected to see associations between decreased activity of the social brain structures and decreased HRV reactivity (H2c).

Methods: Following the protocol from the first study, the participants (n=63, 31F) were invited to take part in a two-session study, with the main procedure utilizing the Future Alone paradigm during the second, neuroimaging session. First, structural images were collected for 7 minutes, which also allowed for obtaining a measure of HRV at rest. Then, participants received either FA or FB feedback regarding their future social relationships, and afterward completed the Social-Nonsocial Affective Task (SNAT) during which they were asked to view social and non-social pictures of either negative or positive valence and react with a button press if the stimulus was repeated (1-back task). During the procedure, the photoplethysmography data (PPG) were recorded to examine the changes of HRV from rest to two consecutive parts of SNAT. Participants were also asked to provide their affect ratings before structural images acquisition, after obtaining feedback, and after SNAT. Furthermore, task-related fMRI included the collection of two localizer tasks, used to define regions of interest (ROI) corresponding to the main social brain regions considered in analyses. The parameter estimates from ROIs for each condition of SNAT were entered into repeated-measures ANOVAs. Change of HRV measured at rest to HRV during SNAT was calculated as the vagal flexibility index and correlated with ROI activations.

Results: In line with Study 1, ratings of negative affect increased after receiving feedback in the FA group, and decreased in the FB group. The positive affect increased significantly after experimental manipulation only in the FB group. We observed a significant change in HF-HRV from rest to the second part of the task in the FB group, and no significant changes between the conditions in the FA group. While all pre-defined ROIs demonstrated sensitivity to social in comparison to non-social conditions, no between-group differences in task-related activation patterns were found. However, an exploratory whole-brain analysis revealed significant clusters of activation within the cerebellum with greater activation in the FB than in the FA group, and increased activation of structures within the visual cortex in the FA compared to the FB group, unspecific to task conditions. Furthermore, a significant association between vagal flexibility index and activation of the left TPJ ($r(56) = 0.334$, $p = .010$) in response to negative social compared to negative non-social scenes was observed. An examination of this effect in each group revealed that this correlation was significant in the FA ($r(26) = 0.492$, $p = .008$), but not in the FB group.

Discussion: Congruently with the results of the first study, both affective and parasympathetic responses were affected by the momentary induction of loneliness. Receiving unfavorable feedback regarding future relationships significantly increased negative affect and decreased vagal flexibility, a pattern which indicates disadaptive physiological response to task engagement. However, the induction of loneliness did not significantly impact neural activity of the main regions linked to the social brain network. Still, we observed an association between vagal flexibility and the activation of the left TPJ, a structure with a crucial role in belief and mental state attribution. As this link was only significant in the FA group, it could be indicative of compensatory response to socioaffective content in response to momentary loneliness.

Study 3: Associations between chronic loneliness and parasympathetic and neural responses

Wiśniewska, M., Piejka, A., Wolak, T., & Okruszek, Ł. (2025). Distinct Fusiform Subregion Activity and Connectivity in Lonely and Non-lonely Individuals During Social Information Processing. *Cerebral Cortex, 35*(7). https://doi.org/10.1093/cercor/bhaf206

Based on the results of the previous two studies, the third study aimed to examine if the affective, parasympathetic and neural responses associated with chronic loneliness differ from the patterns found in relation to momentary loneliness. Firstly, we hypothesized a higher level of negative affect and a lower level of positive affect in the lonely compared to the non-lonely group (H3a). Further, in accordance with the NIM and previous findings from experimental induction studies, we expected to observe decreased vagal flexibility in the lonely in comparison to non-lonely individuals (H3b). A tentative evidence suggesting links between loneliness and altered functioning of the regions associated with the 'social brain' is available. Thus, we hypothesized to observe reduced activity of the structures associated with the mentalizing network, the bilateral TPJ and the mPFC (H4a), as well as decreased functional connectivity between these regions and the AMY (H4b) during social information processing in the lonely in comparison to the non-lonely group. Finally, we hypothesized that vagal flexibility will be associated with decreased activity of the mPFC and the TPJ in the lonely in comparison to non-lonely individuals (H4c).

Methods: The study was preregistered (https://osf.io/vqp8r). One hundred and four participants whose loneliness score was either at the top (lonely individuals LI; n=52, 26F; cutoff point of 49) or bottom (non-lonely individuals, NLI; n=52, 26F; cutoff point of 32) quartile of the R-UCLA distribution (as determined by data from previous projects; available at https://osf.io/8u7m5) were invited to a three-session study. The participants completed a neuroimaging session which included three tasks. Following the protocol from the second study, two localizer tasks were used to define ROIs. Moreover, the main task of the procedure, SNAT, was designed in accordance with the previous study, and extended with pictures of neutral valence. Additionally, at the beginning of the session, participants provided ratings of their current affect. The analyses of ROI activations and HRV changes during the procedure were conducted in correspondence to the protocol of the second study. Moreover, a task-related functional connectivity analysis between ROIs (generalized psychophysiological interaction; gPPI) was conducted. Additionally, between-group differences in neural activation during the SNAT were examined with an exploratory whole-brain analysis, and the clusters of activations which exceeded the cluster-level correction threshold were entered as seeds to an exploratory gPPI analysis.

Results: We observed significantly higher mean negative affect in the LI than in the NLI group, and lower positive affect in LI than in NLI at the beginning of the session. The pattern of HRV changes during the procedure did not differ between the groups, and HF-HRV was higher during rest than during both parts of SNAT. Each ROI considered for analysis demonstrated sensitivity to task conditions (i.e. higher activity for social in comparison to non-social conditions), however, we did not find between-group differences in the patterns of activation, nor a significant association between any of ROIs activation and changes in HRV during the procedure. Whole-brain analysis showed two clusters of activation within the right fusiform face area (FFA) that demonstrated greater activity for social than non-social scenes, with one of the regions with a significant effect for the LI to the NLI group (mid-lateral fusiform gyrus; mFus), and the other for the NLI to the LI group comparison (posterior lateral fusiform gyrus; pFus). Moreover, the gPPI analysis revealed decreased connectivity between the mFus and the region corresponding to the right TPJ for social vs. non-social condition in the LI>NLI comparison.

Discussion: The expected differences between the groups were observed in the affect ratings at the beginning of the procedure. However, the pattern of parasympathetic activity and neural response in pre-defined regions did not significantly differ between lonely and non-lonely individuals. Possibly, the task design, which did not explicitly demand attribution of mental states to presented characters, limited the possibility of reasoning regarding higher-order processing of social information. As we observed between-group differences in activation of the mFus for the lonely in comparison to the non-lonely group, it may indicate a more preferential processing of social content at an earlier-stage of the visual processing pathway in lonelier individuals. The decreased connectivity between the mFus and the right TPJ observed for the same comparison may in turn demonstrate less effective integration of social information in lonely individuals. Furthermore, the greater activation of the pFus to social content for the non-lonely in comparison to the lonely group might suggest the occurrence of less distinct sensitivity during socioaffective processing in lonely individuals.

General discussion

This work examined parasympathetic and neural mechanisms during social information processing in two contexts: experimentally induced momentary loneliness and chronic loneliness. Three consecutive studies provided novel insights into physiological responses linked to loneliness that were only partially congruent with the existing findings and theoretical frameworks used to explain loneliness-related behavioral and physiological mechanisms. As the current work focuses on social information processing, it might also contribute to the understanding of bottom-up social cognitive processes in relation to loneliness.

Behavioral findings

In line with the hypotheses, we observed a significant association between self-reported increased negative and decreased positive affect in both momentary loneliness (H1a), and chronic loneliness (H3a). These results are in line with previously found patterns of reported affect in relation to loneliness (Luo & Shao, 2023). Importantly, the affect scales used in the current work encompassed states usually associated with mental health problems (i.e. feeling worried, low, or abandoned). In this context, the findings appear consistent with the broader body of evidence demonstrating links between loneliness and depression (Matthews et al., 2016), and anxiety (Lim et al., 2016). At the same time, it is important to note that the impact of the experimental induction used in the presented studies on physiological markers might not have been specific to increased feelings of loneliness per se, but to accumulated effects of a more general negative affect. Therefore, the observed effects of momentary loneliness on parasympathetic responding may partially reflect broader mood effects, consistent with previous studies linking HRV reactivity to depressive symptomatology (Schiweck et al., 2019), or increased stress response (Kim et al., 2018).

Parasympathetic findings

All three studies revealed a consistent pattern of parasympathetic responding that occurred alongside mobilization to task-specific demands. In line with H1b, we found that the induction of loneliness, in comparison to social belonging condition, impacted physiological regulation, as evidenced by decreased vagal flexibility from rest to task conditions. Contrary to H1c, an increased skin conductance response associated with sympathetic nervous system functioning was not observed. This result highlights the specificity of the impact of momentary loneliness on parasympathetic activity. Since in all the studies the main task involved social stimuli, these findings suggest that momentary loneliness disrupts physiological regulation during social information processing, thereby impairing the ability to maintain social engagement. However, in contrast to hypothesis H3b and previous findings regarding HRV reactivity in relation to chronic loneliness (Muhtadie et al., 2015; Song et al., 2025), a similar association was not observed in the third study, as the pattern of HRV changes during the procedure did not differ between lonely and non-lonely individuals. This pattern could suggest that the effects of loneliness on adaptive physiological responding may be mainly observed when experienced acutely, and not necessarily as a prolonged condition. While momentary loneliness may act as a social stressor which affects adaptive physiological responding, the presented results show that this pattern cannot be generalized to mechanisms associated with physiological responding in chronic loneliness. It is important to note that the main task of the neuroimaging procedure was relatively easy and might have been sufficient to maintain attention of participants, but not engaging enough to demonstrate complex attentional or inhibitory cognitive effort which could produce robust vagal changes. Therefore, the present findings suggest that lonely individuals may have sufficient regulatory resources to engage with moderately demanding tasks, as evidenced by adaptive HRV reactivity patterns. However, physiological dysregulation may become apparent under conditions of increased cognitive or emotional load.

Neural findings

Despite prior findings linking both momentary (Powers et al., 2013) and chronic (Cacioppo et al., 2009) loneliness to altered functioning in the 'social brain' regions, we have not found differential patterns of social brain activity linked to loneliness in the current work. Contrary to H2b and H4a, we observed no decreased activation of the mPFC and the TPJ in response to social content in relation to loneliness. Of note, previous behavioral studies have also yielded mixed results regarding the association between loneliness and theory of mind abilities (Koerber & Osterhaus, 2020). Since the task used in this work did not require participants to repeatedly take perspective of presented characters, it might have only encompassed processes linked to automatic mentalizing, defined as reflexive mental state attribution that occurs without explicit intention (Satpute & Lieberman, 2006). Hence, this task design might not have enabled the observation of differences in neural basis linked to higher-order theory of mind processes. In turn, while not hypothesized, we found associations between chronic loneliness and distinct patterns of responses to social in comparison to non-social content in two right FFA subregions. The region of the mFus, which demonstrated greater activation in the lonely in comparison to non-lonely individuals, has been previously linked to involvement in the processing of early visual characteristics of stimuli (Rosenke et al., 2021). Moreover, the decreased task-related functional connectivity between the mFus and the right TPJ which was found for social vs. non-social content might also highlight less efficient integration of socioaffective information in more lonely individuals. In contrast, non-lonely individuals demonstrated greater activation of the pFus, the region of the FFA which has been indicated to base higher-order processing of facial stimuli and affective processing (Rosenke et al., 2021). Taken together, these results indicate that chronic loneliness might be associated with differences in bottom-up social stimuli perception, which is the basis of further socioaffective processing. A similar pattern of neural responses was not found for momentary loneliness. Nevertheless, an exploratory investigation allowed for observing greater activation of the clusters of the visual cortex in participants subjected to the loneliness induction. It might corroborate the notion of preferential processing of visual stimuli at earlier stages of the processing pathway as a correlate of loneliness. However, while previous evidence indicated associations between visual cortex activation and preferential processing of negative social stimuli in lonelier individuals (Cacioppo et al., 2009), in the current work the effects occurred on a group level and were not linked to specific stimulus valence or social character. As the induction of loneliness resulted in a generalized increase of negative affect, the observed influence of experimental manipulation on neural correlates of early visual processing might be comparable to previously demonstrated effects of negative affect in facilitating neural processes associated with attention (Kensinger, 2009; Salsano et al., 2024). Conversely, the findings linked to chronic loneliness were observed for social in comparison to non-social stimuli. Thus, it might be suggested that in order to attend to salient social cues, prolonged experience of loneliness leads to more attuned mechanisms associated with preferential processing specific to social information.

Social threat hypervigilance is one of the crucial postulates of the ETL. Nevertheless, the pattern of neural responses observed in the current work did not support the claim that loneliness increases social threat vigilance (H2a, H4b). Neither the induced loneliness nor chronic loneliness were linked to the AMY activation in response to social stimuli in the current line of studies. Moreover, an investigation of between-groups differences in the task-related connectivity patterns between the AMY and regions linked to the 'social brain' also did not yield significant results across the experimental and cross-sectional studies. The link between the AMY and the mPFC functioning has been identified as a central mechanism in both the NIM framework and mental disorder pathophysiology (L. M. Williams, 2016). However, as alterations of these mechanisms were not observed in this work, it could be suggested that automatic encoding of social cues in loneliness is not linked to increased threat perception, but rather to the later-stage interpretation of social information. As chronic loneliness has been linked to both more negative appraisal of social interactions, and of spending time alone (Piejka et al., 2024), biased interpretation of context-sensitive social cues in loneliness may be evident as a wider pattern of behavior. However, the main task used in the neuroimaging studies conducted as part of this work was not sufficient to further test this hypothesis.

Coupling between parasympathetic and neural responses

In accordance with H2c, a significant association between parasympathetic and neural responses was found for momentary loneliness, i.e. vagal flexibility was associated with the left TPJ activation towards negative social in comparison to negative non-social stimuli. While this effect was observed across all participants, the correlation was significant for participants subjected to the loneliness induction, and not for the participants in the social belonging condition. The TPJ is considered an important node of the mentalizing network

(Molenberghs et al., 2016), with a particular role of the left TPJ in responding to contextually-relevant semantic information (Guterstam et al., 2021). Hence, the previously indicated role of the TPJ in physiological regulation (Chang et al., 2013; Miller et al., 2020) suggests that its increased engagement for the social negative content along with sustained parasympathetic response was crucial for attendance to task demands. Moreover, a stronger relationship observed in participants subjected to the induction of loneliness might point towards compensatory regulation of negatively-valenced social content, essential after having received unfavorable feedback regarding one's future relationships. However, contrary to H4c, similar associations between parasympathetic and neural responses were not found for chronic loneliness. Therefore, it may be suggested that momentary loneliness requires an adjusted physiological response to attend to task demands, while a similar response is not visible in more consolidated mechanisms present in chronic loneliness. Furthermore, according to the cognitive control model (Wong et al., 2022), loneliness is associated with compensatory up-regulation of cognitive control networks, which allows for early processing of socioaffective content. Simultaneously, the use of cognitive reserves eventually leads to the exhaustion of resources and results in affective dysregulation. Thus, since momentary loneliness was demonstrated to require initial up-regulation of the TPJ, associated with top-down control, to adjust parasympathetic responses appropriate to process negative social content, the current findings could exemplify this model. However, the lack of the same pattern of parasympathetic and neural responses linked to chronic loneliness further differentiates mechanisms associated with chronic and momentary loneliness observed in relation to social information processing.

Conclusion

Taken together, the current work allows for causal and cross-sectional examination of mechanisms associated with different loneliness levels. The associations between reported affect and both momentary and chronic loneliness were consistent across all three presented studies and are in line with prior evidence of generalized decreased mood related to loneliness (Meng et al., 2020). Still, the current work emphasizes distinct links between physiological responding and loneliness across different time-scales. The results yielded in two studies incorporating experimental manipulation demonstrated robust effects of momentary loneliness on parasympathetic regulation. This pattern suggests that momentary loneliness requires an adjusted physiological response to overcome the brief state of distress in order to adaptively act in the social environment. This notion is supported by the demonstrated relationship between parasympathetic response and increased engagement of regulatory neural mechanisms following momentary loneliness. Conversely, the same methodology revealed no similar associations between physiological responses and chronic loneliness, indicating that mechanisms accompanying momentary loneliness do not extend to chronic loneliness. Moreover, the observed differences in neural correlates of momentary and chronic loneliness also highlighted distinct responses depending on the time-scale. Momentary loneliness elicited increased responses in regions associated with early visual processing, which could have been indicative of attentional processes. In contrast, the effects observed in chronically lonely individuals were specific to social content and may thus accentuate problems with integration of socioaffective information when the social deficiency has been prolonged.

Importantly, despite the links between loneliness and underlying psychophysiological mechanisms which were suggested by the ETL and NIM, most of the hypothesized mechanisms regarding neural activity linked to loneliness were not supported by the current work. While several of the previous studies (e.g. Cacioppo et al., 2009; Powers et al., 2013) found some alterations in the functioning of the 'social brain' regions as a potential mechanism underlying loneliness, evidence for the association between loneliness and alterations of the activity of the main hubs of the social brain (i.e. the mPFC and the TPJ) was not found in the current studies. In turn, the results of the current work might suggest that loneliness is associated with minor alterations in early visual processing. However, these preliminary findings need further investigation. As the results presented in the current work do not support the neural architecture congruent with the ETL, or the generalized conceptualization of the mechanisms linked to loneliness, i.e. heightened activation of bottom-up threat signalling which is not countered by the top-down mechanisms (L. M. Williams, 2016), different approaches for investigating neural mechanisms associated with loneliness were proposed. Notably, the cognitive control model (Wong et al., 2022) might provide an important framework for understanding the socioaffective processing in loneliness, as it links early perceptual processes to the dynamics of the cognitive control networks functioning. Moreover, the mechanisms underlying loneliness could also be considered in relation to the social baseline theory (Beckes & Coan, 2011), which emphasizes that social proximity aids in physiological metabolic resources management, and a lack of close social relationships might increase the costs of engaging with the environment. Nevertheless, more evidence is required to further connect loneliness to its underlying biological mechanisms.

Limitations

Although the current work provides evidence for differences between mechanisms underlying momentary and chronic loneliness by accumulating the complementary data across three studies utilizing corresponding methodologies, several limitations can be pointed out. The data regarding participants' loneliness level were gathered before the start of each study and were based on R-UCLA score. However, R-UCLA does not specify the duration of time period regarding experienced loneliness, which could be to some extent influenced by situational circumstances (W. Chen et al., 2019; Conti et al., 2023). Thus, in the current work it was not possible to examine whether the reported level of loneliness was associated with a lasting pattern of physiological responding, or whether the reported loneliness level was not experienced over a prolonged time period and hence did not reflect consolidated mechanisms hypothesized in relation to chronic loneliness. Therefore, future work should incorporate pronounced longitudinal designs to account for the possibility of capturing a situationally-dependent feelings of loneliness. Additionally, in the current work, the association between sympathetic activity and loneliness was investigated only in relation to momentary loneliness. Even though we did not observe a significant impact of momentary loneliness on skin conductance level during social information processing, these associations could be further investigated in relation to chronic loneliness. Importantly, the main task used in the fMRI studies presented in the current work allowed to focus on differences in processing of social in comparison to non-social content of different valence in relation to either momentary or chronic loneliness. Nevertheless, the task might have elicited processes connected to automatic mentalizing. Therefore, it did not enable a clear disambiguation of bottom-up and top-down processes in relation to loneliness, which could be addressed in future studies. Moreover, an additional investigation of effects linked to low- and high-effort cognitive tasks performance could also further enable a comparison of neural and accompanying parasympathetic responses in association with loneliness. Furthermore, the tasks used as part of this work were based on static stimuli which do not resemble real social situations. Therefore, future work should incorporate approaches with higher ecological validity to enable investigating psychophysiological mechanisms underlying loneliness in naturalistic social interactions.

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Brief induction of loneliness decreases vagal regulation during social information processing

Aleksandra Piejka [a,1], Marcelina Wiśniewska [a,1], Julian F. Thayer [b,c], Łukasz Okruszek [a,*]

[a] Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Poland
[b] Department of Psychological Science, 4201 Social and Behavioral Sciences Gateway, University of California, Irvine, United States of America
[c] Department of Psychology, The Ohio State University, United States of America

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ABSTRACT

Perceived social isolation, or loneliness, has been repeatedly linked to numerous adverse health outcomes. Much effort has been directed towards elucidating the mechanisms underlying its effects on the cardiovascular system, which may explain the deleterious effects on morbidity and mortality. It has been previously suggested that perceived social isolation can impair effective parasympathetic regulation and physiological adjustment to the demands of the social environment. Thus, the present study aimed at investigating the causal impact of an induction of loneliness on vagal activity during social stimuli processing. In the study, participants (N = 119) were led to anticipate either a future filled with satisfying relationships (Future Belong) or a lonely life (Future Alone). Then, they were asked to complete an implicit emotion regulation task while their cardiovascular activity was recorded.

In the Future Belong group, a pattern of vagal suppression was observed between the resting period and task completion, which was followed by vagal recovery during the post-task resting period. However, in the Future Alone group, a change from the baseline HRV was observed only at the beginning of the task, but not during its consecutive stages. Moreover, in participants who believed in the given FA feedback, the initial vagal suppression was absent. These findings provide evidence that even a brief induction of loneliness can result in a blunted vagal suppression during social information processing. It can be hypothesized that the lack of the ability to regulate vagal activity while processing social cues may potentially underlie problems with social engagement and self-control.

1. Introduction

The last two decades were marked by an increased scientific inquiry into the consequences of perceived social isolation (PSI), popularly referred to as 'loneliness', on multiple health outcomes (Cacioppo and Cacioppo, 2018). It has been repeatedly shown that the subjective mismatch between one's actual and desired social relationships may have deleterious effects on the quality of mental, physical, and social functioning even in the absence of objective isolation. Lonelier healthy adults are more likely to experience mental health problems, engage in physical health risk behaviors, and be unemployed compared to non-lonely peers (Matthews et al., 2019). Loneliness is currently recognized as a standalone risk factor for cardiovascular diseases, which are the leading cause of death globally (Holt-Lunstad et al., 2015); it was also found to be a significant predictor of both general cognitive impairment and development of Alzheimer's disease (Wilson et al., 2007). Multiple possible mechanisms have been proposed to mediate the effects of PSI on health, e.g., loneliness was shown to be linked with decreased viral immunity (Cole et al., 2015), to promote pro-inflammatory responses (Jaremka et al., 2013), and to decreased telomere length (Wilson et al., 2019) in the general population. Thus, given its growing prevalence (Cigna, 2018) and the profound consequences for physical and social well-being, an extensive examination of psychological and physiological mechanisms underlying PSI has been highlighted as crucial for establishing successful interventions to reduce their impact (Hawkley and Cacioppo, 2010; Cacioppo and Cacioppo, 2018; Masi et al., 2011; Heinrich and Gullone, 2006; Mushtaq et al., 2014).

A theoretical framework proposed by Cacioppo and Cacioppo (2018)

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[*] Corresponding author at: Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Jaracza 1, 00-378 Warsaw, Poland.
E-mail address: lukasz.okruszek@psych.pan.pl (Ł. Okruszek).

[1] Authors contributed equally.

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offers a hypothetical explanation for those mechanisms: bereft of reliable connections which are crucial for survival, lonely individuals direct their cognitive efforts to self-preservation, self-centeredness, implicit vigilance and avoidance of potential threats. Studies examining lonely (vs non-lonely) individuals provided empirical evidence for the heightened sensitivity to socially threatening stimuli (for a review, see: Spithoven et al., 2017). Such bias, in turn, can result in the rigidity of negative response to social encounters and increased difficulty with emotion regulation during interpersonal interactions (Cacioppo and Cacioppo, 2018). Consequently, loneliness reduces available cognitive resources and prevents one from applying top-down mechanisms necessary for efficient self-regulation and emotional adjustment.

While it is difficult to experimentally validate the causal role of loneliness due to its highly subjective character, a paradigm proposed originally by Twenge et al. (2001) offers a method of evoking a feeling of aloneness in laboratory conditions. During the experiment, participants received information that they can expect to maintain satisfying and caring relationships through their life (Future Belong) or they are told that their social bonds probably will not last and that they might end up alone in life (Future Alone).

Even though the paradigm is usually described as induction of social exclusion, the content of the manipulation refers explicitly to the state of loneliness and the lack of stable and nurturing relations, not to the ostracism or rejection per se. Unlike other paradigms aimed at evoking social exclusion, the Future Alone paradigm is not based on creating the actual or imaginary situation where one is confronted with dislike, hostility, omission or judgment from other people (for a review of the most established paradigms, see: Wirth, 2016). Moreover, it has been recognized as the most accurate method of inducing an impression of a long-term condition rather than a momentary state (Wirth, 2016). Research using the procedure provided evidence that the prospect of a lonely future can cause a decrease in self-regulatory capacity (Baumeister et al., 2005), prosocial behavior (Twenge et al., 2007), and cognitive abilities (Baumeister and DeWall, 2005), and it can reinforce aggressive reactions (Twenge et al., 2001) and emotional numbness (DeWall and Baumeister, 2006). Those findings support the hypothesized causal link between PSI and self-regulation deficits. However, it remains unclear what exact psychophysiological processes underlie this relationship.

Potential explanation of the physiological mechanisms elicited by PSI comes from the literature on parasympathetic regulation, and, more specifically, the activity of the vagus nerve. A growing body of research suggests that the inability to interpret social cues adequately and to regulate emotions in adjustment to social context can be reflected by decreased phasic vagal activity (e.g., Muhtadie et al., 2015; Park et al., 2014). Phasic vagal activity, or vagal suppression, can be defined as a dynamic modulation of control exerted by the vagus nerve on the heart in response to demands of the environment and is indexed by an event- or a task-related decrease in heart rate variability (HRV). Kemp et al. (2017) proposed that reciprocal causality between changes in heart rate variability and the subjective experience of environmental stressors promotes either beneficial or maladaptive psychophysiological processes in the long term.

In line with these assumptions, decreased vagal control was linked to reduced attention and affective regulation (Thayer and Lane, 2000), negative social interactions and stress (Shahrestani et al., 2015), lower social engagement and self-regulation (Geisler et al., 2013), and numerous clinical disorders (Kemp and Quintana, 2013).

While the research directly investigating both loneliness and dynamic changes in HRV is scarce, PSI was found to negatively correlate with vagal suppression in response to cognitive tasks (Muhtadie et al., 2015) and to moderate the relationship between vagal reactivity and intranasal oxytocin (Norman et al., 2011). Importantly, this relationship could help to explain the corrosive effect of PSI on physical health (Xia and Li, 2018). Decreased vagal regulation has been previously linked to inflammatory markers (Jarczok et al., 2015), a heightened risk of coronary heart disease (Thayer et al., 2010), decreased stress recovery (Baert et al., 2012), and accelerated cellular aging (Wilson et al., 2019). However, although it is believed that dynamic changes in vagal activity better reflect responses to the ever-changing social world, most of the studies in the field focused solely on resting vagal tone and have not investigated changes in phasic HRV in response to environmental factors or task demands (c.f. Muhtadie et al., 2015, Park et al., 2014). The detrimental effects that loneliness may have on the ability to dynamically regulate psychophysiological response to social stressors thus remain understudied.

The main aim of the present study is to examine the causal effects of PSI induction on vagal control during a task requiring processing and reappraisal of social stimuli. We hypothesized that participants who were subjected to the experimental induction of loneliness would demonstrate a reduced ability to adjust their response to context-sensitive social information. The reduction of the regulatory capacity would be reflected in blunted vagal reactivity indexed by a smaller change in HRV during the task. At the same time, we expected that the participants subjected to the experimental induction of loneliness will exhibit more stress response to negative social stimuli (reflected by increased skin conductance level). Furthermore, we expected the participants subjected to the PSI induction 1) to perceive socially threatening stimuli as more negative during the context-free observation of the stimuli, and 2) to display less effective implicit regulation to contextual cues linked to social stimuli. The latter would be indicated by the smaller change in behavioral ratings from spontaneous observation to context-dependent condition.

In order to minimize the age-related variance in HRV (Voss et al., 2012), the study focused on the sample of young adults (age 18–35). This group is also of particular concern for the research on PSI, given that in recent years it has been recognized as being particularly prone to loneliness and its consequences (e.g. Beam and Kim, 2020; Shovestul et al., 2020).

2. Methods

2.1. Participants

Participants for the study were recruited via social media groups. Candidates completed an online survey containing a set of screening and demographic questions together with additional measures such as the Polish version of the Revised UCLA Loneliness Scale (R-UCLA; Kwiatkowska et al., 2015). The inclusion criteria for the study were as follows: i) age in the 18–35 range, ii) no history of psychiatric or neurological disorders, substance abuse, and cardiovascular diseases, iii) dysphoria score < 12 and anhedonia score < 9 as measured by the Polish version of the revised Center for Epidemiologic Studies Depression Scale (CESD-R; Koziara, 2016), iv) Body Mass Index (BMI) < 30, v) being a native-speaker in the Polish language, and vi) not having a psychology degree nor being a psychology student above the first year (to minimize the risk of recognizing the experimental manipulation as bogus).

One-hundred twenty-eight participants fulfilled the inclusion criteria and were invited to take part in the two-session study at the Institute of Psychology, Warsaw. Due to technical problems, one participant's data could not be used in the analysis. Therefore, the final sample consisted of one hundred and twenty-seven participants (74F; mean age: 23.87y ± 4.81). The majority of the group reported having obtained secondary education ($N = 75$) or higher education degree ($N = 50$), and two participants reported finishing primary education.

The sample size for the current study was calculated using the pwr package in R. It was determined that to detect a medium effect size (Pearson's $r = 0.3$) with power 0.85, at least 96 participants were required.

All participants provided informed written consent prior to participation in the study and were reimbursed 50 PLN for completing each session (100 PLN total). The study protocol was approved by the Ethical

Committee at the Institute of Psychology, Polish Academy of Sciences.

2.2. *Procedure*

During the first session, participants were informed that the study aimed at investigating associations between social functioning, personality, and psychophysiological correlates of social information processing. Moreover, in order to reinforce the credibility of the upcoming experimental manipulation, they were told that data gathered during the session would be later used to create personalized descriptions on them, which would be presented during the following meeting. Then, participants completed a battery of behavioral tasks measuring social cognitive skills and a set of self-report questionnaires, which are beyond the scope of the present study. The set of measures included the Polish version of the revised Eysenck Personality Questionnaire (EPQ-R; Jaworowska, 2012), which was used to provide feedback during a subsequent session.

Between the two sessions, there was a break of at least one day. Before taking part in the second session, participants were asked to abstain from psychoactive substances and intensive exercises on the day before and not to drink coffee or smoke an hour before the examination, as these factors might influence HRV assessment (Quintana and Heathers, 2014). The course of the entire session is presented in Fig. 1. At the beginning of the second part of the study, participants were told that the aim of the session was to examine “the extent to which their knowledge about themselves and other people influences behavioral and psychophysiological markers of social information processing”. At the beginning of the main procedure, participants were asked to provide ratings of their current level of positive (confident, relaxed, excited, cheerful, interested) and negative (angered, lonely, sad, anxious, stressed) affect on Likert-type scales (1–5). Next, a 6-minute baseline recording began, during which the participants were asked to relax and sit quietly with their eyes focused on a fixation point displayed on the screen.

After the baseline recording, participants were randomly assigned to one of the two experimental conditions based on the well-established experimental paradigm proposed by Twenge et al. (2001): Future Alone feedback (FA; N = 66, 41F) or Future Belong feedback (FB; N = 61, 33F). The exact wording of the manipulation and its English translation can be found in the Supplementary file. In order to increase the believability of the manipulation, the first part of feedback described the participant’s extraversion level and was based on an actual EPQ-R score of each participant. The feedback was presented to participants in the form of five consecutive blocks of text, each displayed for 15 s. The information regarding the extraversion level was similarly distributed between two groups ($\chi^2(2, N = 127) = 2.52, p > .05$). Next, participants provided affect ratings once again. Then, they were asked to complete the Emotion Regulation Task (ERT; see details in Section 2.3). Upon completion of the ERT, self-reported affect was examined for the last time, and participants were asked to relax for a 6-minute post-task rest period during which ECG was still recorded. Finally, participants rated whether the feedback they received was accurate (1 - Definitely not accurate, to 7 - Definitely accurate).

Participants were debriefed immediately after the procedure, and an investigator ensured that they understand that the feedback concerning their relationships was assigned randomly and was not based on any information provided by them.

2.3. *Emotion Regulation Task (ERT)*

The task included a presentation of 40 neutral and 120 angry faces from the FACES database (Ebner et al., 2010) and was modeled based on the reappraisal task from Morawetz et al. (2016). Half of the stimuli displayed female and half male faces, and it presented individuals from three age categories: young, middle, and old. During the Observe condition, participants were asked to passively view faces with either neutral or angry expressions. During the remaining two conditions participants were presented with angry expressions only and were informed to react to the photos as if the depicted person 1) was someone they know personally and who was angry at them (Increase) or 2) was a stranger who had a bad day (Decrease). Increase and Decrease conditions were presented to participants in a counterbalanced order. The participants were asked to rate their feelings concerning each person using the 9-point scale. The scheme of each ERT trial is presented in Fig. 1.

All participants completed a training session with eight trials (2

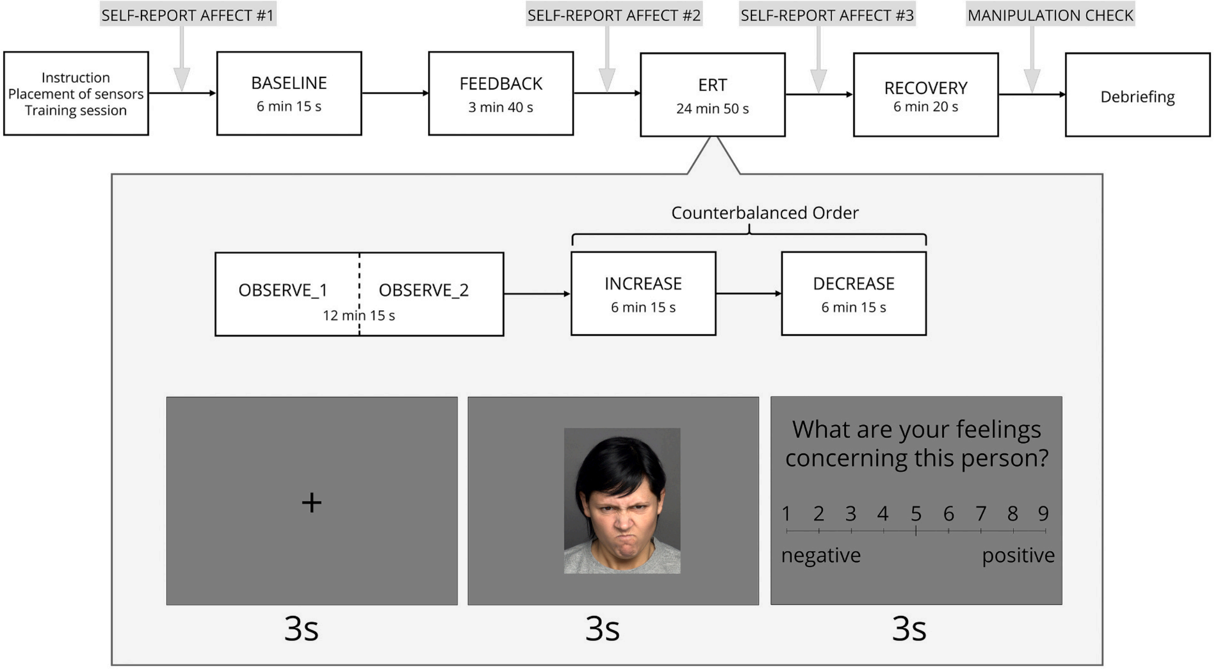

Fig. 1. The course of the second session and the structure of Emotion Regulation Task (ERT) with a sample trial.

Observe, 3 Decrease, and 3 Increase trials). The task was designed using the NBS Presentation (version 21.1).

2.4. Physiological signal recording and preprocessing

Physiological measures were collected using Biopac MP150 Starter Systems for Windows and AcqKnowledge (version 4.4.2) data acquisition software (BIOPAC Systems Inc.; Goleta, California; USA). ECG signal was recorded using an ECG100C amplifier (with 1000 signal gain, low pass filter of 35 Hz, and high pass filter of 1.0 Hz) with sensors placed in modified Lead II configuration. Skin conductance level was obtained by using GSR100C amplifier (with 5 μS/V signal gain, 10 Hz low pass filter, and DC high pass filters) with two Ag-AgCl electrodes filled with isotonic gel and placed on distal phalanges of the index and middle finger on the participant's left hand. The direct constant current was applied. All the signals were sampled at a frequency of 2000 Hz. In addition, photoplethysmography (PPG) data was collected. However, in the present study, only ECG data was used as it has been shown that under a state of mental stress PPG data can deviate from the ECG signal to an unacceptable extent (Schäfer and Vagedes, 2013). During the procedure, the participants were asked to stay seated, minimize their movements, to keep their left hand on the desk and not to cross their legs during the measurement. The recording was done in a dimly-lit laboratory, and participants were given earplugs in order to homogenize experimental conditions and minimize potential distractions.

2.5. Data preparation and preprocessing

Six 5-minute segments corresponding to the main parts of the study [baseline, observe 1, observe 2, increase, decrease, recovery] were extracted for further analysis.

After a visual inspection, the cardiovascular data were further preprocessed and analyzed in Kubios HRV Premium software (version 3.3.1). Data were detrended using a smoothness priors approach ($\lambda = 500$) and the automatic artifact correction algorithm was applied with a medium threshold value.

High-frequency HRV values were obtained by using the autoregressive spectrum method with the 0.15–0.4 Hz band, and log-transformed HF-HRV (logHF-HRV) was used for further analysis in line with guidelines and recommendations for HRV data analysis (Berntson et al., 1997; Laborde et al., 2017; Malik et al., 1996), and the methodology of previous studies investigating phasic HRV changes (e.g. Berna et al., 2014; Park et al., 2014; Spangler et al., 2018). The GSR data were first downsampled to 100 Hz and smoothed by using an adaptive Gaussian filter. Then, the signal was divided into tonic and phasic components with the Continuous Decomposition Analysis (CDA) method implemented in Ledalab software (version 3.4.9) (Karenbach, 2005). The mean level of tonic Skin Conductance Level (SCL) was calculated for each condition.

2.6. Statistical analysis

In order to examine to what extent the experimental manipulation influenced participants' negative and positive affect, two repeated-measures ANOVAs were calculated with Time (baseline, post-manipulation, recovery) as a within-subject factor and Group (FA, FB) as a between-subject factor. In addition, to further investigate the effects of the experimental induction of loneliness, for each individual item from the positive and negative affect scales a repeated-measures ANOVA was calculated with Time (baseline, post-manipulation, recovery) as a within-subject factor and Group (FA, FB) as a between-subject factor.

Moreover, differences in mean ratings of the ERT stimuli between conditions were analyzed using a repeated-measures ANOVA, with Condition (Observe neutral, Observe angry, Increase, Decrease) as within-subject factors and Group (FA, FB) as a between-subject factor.

In order to examine changes in the physiological responses to the task, two repeated-measures ANOVAs with Condition (baseline, observe 1, observe 2, increase, decrease, recovery) as a within-subject factor and Group (FA, FB) as a between-subject factor were performed separately for HF-HRV and SCL data.

Participants who had more than 5% of artifacts in each of the six extracted segments and two extreme outliers (scores equal or more than three interquartile range in the baseline segment of HRV and SCL signal) were excluded. Thus, all the analyses were conducted on a sample of 119 participants (FA: N = 62, 39F, age: 24.1 ± 5.2, FB: N = 57, 31F, age: 24.6 ± 4.4). Groups did not differ significantly with regard to sociodemographic characteristics (age: t(117) = 0.59 p = .56; gender: χ^2(2, N = 119) = 0.89, p = .35; education: χ^2(2, N = 119) = 1.77, p = .41), nor trait loneliness (t(117) = −1.40, p = .17) or level of extraversion (t(117) = 1.29, p = .20).

The analyses described above were also repeated on the subset of 91 participants who declared that feedback provided during the procedure was accurate (ratings above four on the 7-point scale; FA: N = 43, 23F, age: 24.5 ± 5.3; FB: N = 48, 26F, age: 23.7 ± 4.3). Again, groups did not differ significantly with regard to sociodemographic characteristics (age: t(89) = 0.76 p = .45; gender: χ^2(2, N = 91) = 0.01, p = .95; education: χ^2(2, N = 91) = 2.13, p = .34), nor trait loneliness (t(89) = −0.23, p = .82) or level of extraversion (t(89) = 0.89, p = .38).

3. Results

3.1. Behavioral results

3.1.1. Manipulation check

The mean ratings of feedback received by the participants in both groups were on average above the middle point (5.28 ± 1.59), indicating that participants tended to perceive the feedback as accurate. In line with the original work using the experimental paradigm adopted in the present study (Baumeister et al., 2005), we found that participants in the FA group rated the feedback received as less accurate (4,87 ± 1.62) than participants in the FB group (5.72 ± 1.44; t(117) = −3.01, p < .01, d = 0.45).

3.1.2. Positive affect

We observed a main effect of Time (F(2,116) = 35.04, p < .01, ηp2 = 0.23), with a significantly higher level of positive affect at baseline (2.81 ± 0.54) and post-manipulation (2.76 ± 0.55) compared to recovery (2.49 ± 0.58; p < .001). No between-group differences were found (F(1,117) = 0.083, p = .774, ηp2 < 0.001). However, an interaction between Time and Group (F(2,116) = 3.27, p = .04, ηp2 = 0.03) was observed. Pairwise comparisons (Bonferroni corrected) revealed higher positive affect in the FA group at baseline (2.85 ± 0.54) than post-manipulation (2.7 ± 0.57; p = .02), and significantly lower positive affect in the FA group at recovery (2.47 ± 0.53) than at both baseline (p < .001) and post-manipulation (p < .001). In the FB group the positive affect was significantly higher at baseline (2.76 ± 0.55) and post-manipulation (2.82 ± 0.52), than at recovery (2.51 ± 0.63; p < .001).

The analysis was then repeated on the subset of subjects who perceived the received feedback as accurate. The main effect of Time (F(2,88) = 30.99, p < .01, ηp2 = 0.26) remained significant, and higher level of positive affect at baseline (2.81 ± 0.51) and post-manipulation (2.78 ± 0.51) than during the recovery (2.47 ± 0.55; p < .001) was observed. No main effect of Group (F(1,89) = 0.072, p = .789, ηp2 < 0.001) nor interaction between Time and Group (F(2,88) = 1.79, p = .17, ηp2 = 0.02) were found.

The analyses for each individual item from the scale revealed significant interactions between Time and Group for cheerfulness (F(2,116) = 5.41, p = .005, ηp2 = 0.044) and interest (F(2,116) = 5.83, p = .003, ηp2 = 0.047), with lower level of cheerfulness and higher level of interest in the FA group than in the FB group post-manipulation. The effects were replicated in the subset of participants who rated the received feedback as accurate. A detailed description of the analyses for individual items from the positive scale can be found in the Supplementary materials.

3.1.3. Negative affect

No main effect of Time (F(2,116) = 1.54, p = .22, ηp2 = 0.013) nor Group (F(1,117) = 1.19, p = .28, ηp2 = 0.010) were observed. However, a significant interaction between these factors was found (F(2,116) = 11.95, p < .001, ηp2 = 0.09), with no between group differences at baseline (FA: NA = 1.53 ± 0.57 vs FB: NA = 1.67 ± 0.62 p = .21) or during the recovery (FA: NA = 1.66 ± 0.64 vs FB: NA = 1.53 ± 0.53 p = .24), but a higher level of negative affect in the Future Alone group (1.84 ± 0.78) when compared to the Future Belong group (1.50 ± 0.58) post-manipulation (p < .01).

The analysis was then repeated on the subset of subjects who rated received feedback as describing them accurately. Again, no main effect of Time (F(2,88) = 1.86, p = .16, ηp2 = 0.021) nor Group (F(1,89) = 1.41, p = .24, ηp2 = 0.016) were observed. The interaction between these factors remained significant (F(2,88) = 10.26, p < .001, ηp2 = 0.10). There were no differences between the groups at baseline (FA: NA = 1.52 ± 0.50 vs FB: NA = 1.63 ± 0.61, p = .36) or during the recovery (FA: NA = 1.65 ± 0.59 vs FB: NA = 1.54 ± 0.55, p = .36), while a higher level of negative affect was observed in the FA group (1.88 ± 0.84) when compared to the FB group (1.48 ± 0.58) post-manipulation (p < .01).

The analyses of the individual items from the scale showed significant interactions between Time and Group for anger (F(2,116) = 3.18, p = .043, ηp2 = 0.03), sadness (F(2,116) = 11.04, p < .001, ηp2 = 0.09) and anxiety (F(2,116) = 5.83, p = .003, ηp2 = 0.05), with higher levels of anger, sadness and anxiety observed post-manipulation in FA compared to FB participants. Furthermore, a higher level of anger was observed in FA compared to FB participants also during recovery. Finally, participants in the FB group reported higher levels of sadness compared to FA participants during the baseline.

Then, the analyses were repeated for the subset of subjects who perceived the feedback as accurate. The pattern of effects observed in the whole set of participants was observed in the subset for sadness and anxiety, while there was no interaction for anger. However, in this subset of participants we have also observed an interaction between Time and Group for loneliness (F(2,88) = 3.39, p = .04, ηp2 = 0.037), with higher level of post-manipulation loneliness in the FA group than in the FB group. A detailed description of the analyses for individual items from the negative scale can be found in the Supplementary materials.

3.1.4. ERT ratings

We observed a main effect of Condition (F(3,115) = 350.66, p < .001, ηp2 = 0.75). Post-hoc pairwise comparisons (Bonferroni corrected) showed that faces from the Observe neutral condition were rated on average more positively (5.26 ± 0.46; p < .001) than angry faces presented throughout the remaining task conditions, and faces from the Decrease condition (4.13 ± 0.68) were on average rated more positively than faces from the Observe angry (3.49 ± 0.71; p < .001) and Increase (3.39 ± 0.77; p < .001) conditions. Ratings of the two latter conditions did not differ significantly (p = .47).

No between-group differences (F(1,117) = 0.04, p = .95, ηp2 < 0.001) nor interaction between Condition and Group (F(3,115) = 0.99, p = .4, ηp2 = 0.008) were found.

In addition, the analysis repeated on the subjects who rated the feedback as accurate replicated the effects observed in the full sample. While we observed no between-group differences (F(1,89) = 0.49, p = .49, ηp2 = 0.005) nor interaction between Condition and Group (F (3,87) = 0.54, p = .66, ηp2 = 0.006), the main effect of Condition (F (3,87) = 303.82, p < .001, ηp2 = 0.77) remained significant. Post-hoc pairwise comparisons (Bonferroni corrected) revealed the same pattern of the ratings in this subset of participants. Faces from the Observe neutral condition were rated on average more positively (5.25 ± 0.38; p < .001) than angry faces, with faces from the Decrease condition (4.08 ± 0.63) being on average rated more positively than faces from the Observe angry (3.48 ± 0.68; p < .001) and Increase (3.37 ± 0.70; p < .001) conditions. Ratings of the two latter conditions also did not differ significantly (p = .48) in this sample.

3.2. Heart rate variability

We found the main effect of Condition to be significant (F(5,113) = 25.74, p < .001, ηp2 = 0.18): post-hoc pairwise comparisons (Bonferroni corrected) revealed that logHF-HRV was higher during both baseline (6.34 ± 1.04) and recovery (6.40 ± 0.97) as compared to the rest of conditions (p < .01). Also, logHF-HRV during the decrease condition (6.19 ± 0.93) was higher than during the first part of the observe condition (6.07 ± 0.92; p = .01). Other differences between conditions were not significant.

While the main effect of Group was not significant (F(1, 117) = 0.01, p = .94, ηp2 < 0.001), a significant interaction was observed between Condition and Group (F(5,113) = 3.42, p < .05, ηp2 = 0.03). Pairwise comparisons (Bonferroni corrected) revealed that the effect was caused by within-group differences between conditions. In the FB group logHF-HRV during baseline (6.41 ± 1.06) and recovery (6.44 ± 0.97) was significantly higher than during all other conditions (observe 1: 6.05 ± 0.93, p < .001; observe 2: 6.09 ± 0.963, p < .001, increase: 6.11 ± 0.933, p < .001; decrease: 6.12 ± 0.973, p < .001). No other differences were found significant.

On the contrary, in the FA group, logHF-HRV during baseline (6.28 ± 1.02) differed only from observe 1 condition (6.09 ± 0.91, p = .042). LogHF-HRV during observe 1 condition was also significantly lower from decrease (6.25 ± 0.89, p < .01) and recovery (6.36 ± 0.98, p < .001) conditions. Finally, the logHF-HRV level during recovery was also significantly higher than during observe 2 (6.15 ± 0.90, p = .001) and increase (6.17 ± 0.91, p = .001) conditions.

Again, we repeated the analysis on the sample of participants who rated received feedback as accurate. The main effect of Condition was again found significant (F(5, 85) = 16.72, p < .001, η2 = 0.16). Post-hoc Bonferroni corrected comparisons corroborated the previously found differences. LogHF-HRV was higher during baseline (6.37 ± 1.02, p < .05), and recovery (6.44 ± 0.96, p < .001) as compared to the rest of conditions except for decrease condition (6.20 ± 0.90) which was not significantly different from baseline (p = .055). The main effect of Group remained non-significant (F(1,89) = 0.01, p > .05, ηp2 < 0.001).

Again, the interaction effect was observed (F(5,85) = 2.93, p < .05, ηp2 = 0.03). The pattern of results in the FB group was the same as in the full group analysis. However, a significant change in results was found in the FA group: logHF-HRV during baseline (6.28 ± 1.05) did not differ significantly from any other condition and logHF-HRV during recovery (6.42 ± 1.04) was higher (p ≤ .01) as compared to all other conditions except baseline and decrease condition (6.26 ± 0.92) (Fig. 2).

3.3. Skin conductance level

The main effect of Condition (F(5, 113) = 22.96, p < .001, ηp2 = 0.16) was found to be significant. Mean SCL was significantly lower during the baseline (5.99 ± 2.62) as compared to other conditions (observe 1: 6.66 ± 2.85, p < .001; observe 2: 6.52 ± 2.87, p < .001; increase: 6.47 ± 2.75, p < .001; decrease: 6.51 ± 2.83, p < .001; recovery: 6.34 ± 2.73, p < .01). The difference in SCL was also significant between observe 1 and observe 2 conditions (p = .04), and between recovery condition and observe 1 (p < .01) and decrease conditions (p = .02). The main effect of Group (F(1,117) = 0.54, p > .05, ηp2 = 0.005) and interaction effect (F(5,113) = 2.72, p = .06, ηp2 = 0.02) were not significant.

Again, the analysis was repeated on the sample of participants who rated received feedback as accurate. The main effect of Condition (F(5, 85) = 14.56, p < .001, ηp2 = 0.14) remained significant. Post-hoc pairwise comparisons (Bonferroni corrected) revealed that SCL was significantly lower during baseline (6.02 ± 2.67) than during other

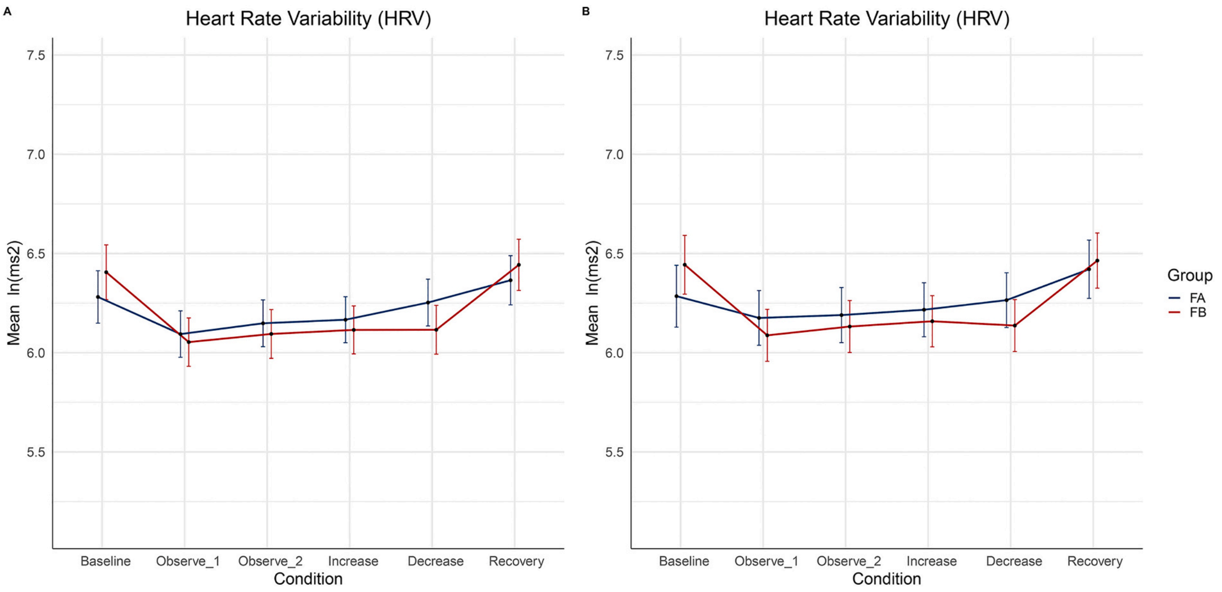

Fig. 2. Mean HRV across conditions in all participants (left) and participants who rated feedback as accurate (right).

conditions (observe 1: 6.66 ± 2.92, p < .001; observe 2: 6.50 ± 2.92, p < .001; increase: 6.44 ± 2.79, p = .001; decrease: 6.47 ± 2.88, p < .001) except for recovery (6.33 ± 2.79, p = .1). There was also a significant difference between observe 1 and recovery (p = .05). No significant effects of Group (F(1,89) = 1.70, p > .05, ηp2 = 0.02) or interaction between factors (F(5,85) = 1.01, p > .05, ηp2 = 0.01) were found (Fig. 3).

4. Discussion

The current study aimed to examine the causal effects of the induction of loneliness on vagal regulation during social cues processing. On the level of behavioral ratings, we observed predicted changes between subsequent stages of the main task. While no effects of the induction were found on explicit appraisals of social cues, in line with our initial hypothesis, the analysis of HRV corroborated the implicit impact of the loneliness induction on participants' autonomic responses.

In the FB group, participants' HRV decreased significantly from baseline to the first part of the task, maintained at a similar level during the task and, then returned to the baseline level during post-task rest. This pattern of HRV changes may be indicative of a task mobilization and recovery and is in line with previous observations of vagal suppression in tasks requiring attentional, regulatory, or cognitive effort (Muhtadie et al., 2015; Graziano and Derefinko, 2013; Sulik et al., 2015; Movius and Allen, 2005; Zhang et al., 2015). Notably, the task was presented not as an explicit emotion reappraisal task but as a measurement of the influence of given information on participants' evaluation of self and other people. It thus required continuous attentional effort and activation of processes related to self-reflection and emotional awareness (Morawetz et al., 2016), so it can be assumed that the task-related decrease in HRV reflected engagement in the procedure.

Importantly, we found a different pattern of physiological response in the FA group. While at the beginning of the task FA participants reacted with a decrease in HRV similarly to participants from the FB group, after the first part of the Observe condition the average HRV level in the FA group returned to the baseline and did not significantly change

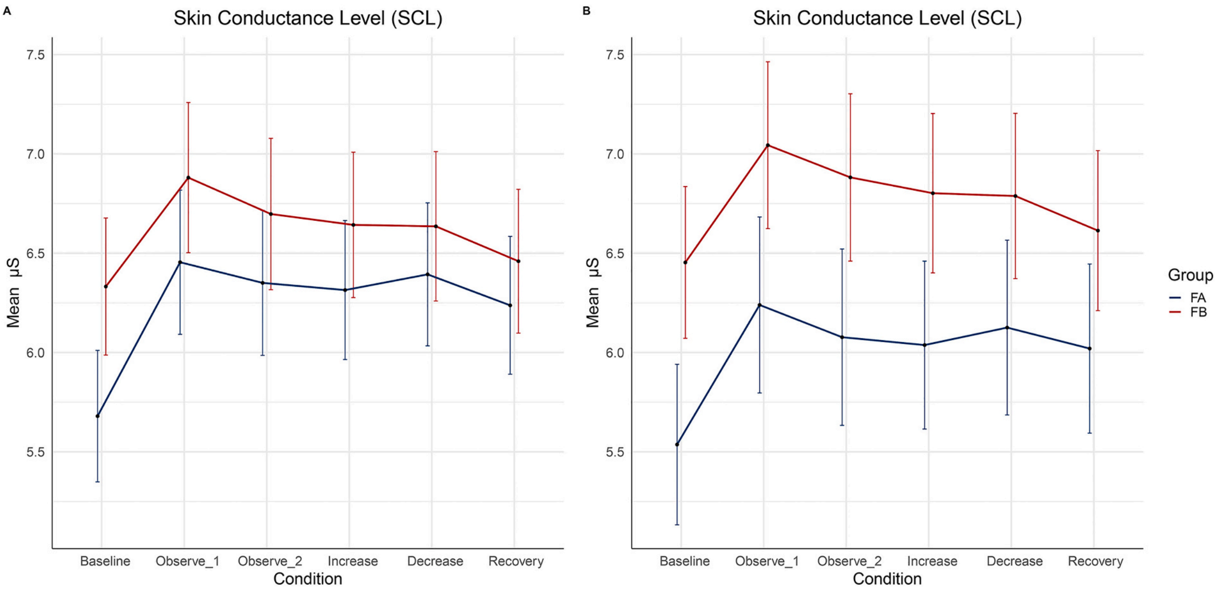

Fig. 3. Mean SCL across conditions in all participants (left) and participants who rated feedback as accurate (right).

till the end of the procedure. Moreover, when the analysis was repeated only on the participants who believed in the given feedback, there was no significant change between the baseline level of HRV and any subsequent stages of the task in the FA group.

It is important to note that while the main aim of the induction was to elicit the feeling of loneliness in laboratory settings, the analysis of behavioral responses to the manipulation revealed a more complex pattern of impact of the manipulation on participants' positive and negative emotions.

The experimental feedback resulted in a transient increase in emotions usually associated with loneliness (i.e. sadness and anxiety), lower cheerfulness and higher anger and interest (which could be provoked by confronting unpleasant and unexpected information) in the FA group as compared to the FB group. Importantly, after excluding participants who rated the feedback as not accurate, the difference in cheerfulness, interest, sadness and anxiety remained significant between experimental conditions, but the groups also differed in the levels of declared post-manipulation loneliness. Moreover, the FA participants who believed in the feedback did not exhibit the initial vagal suppression observed when all of the participants were included in the sample.

The previous findings provide evidence for positive effects of cheerfulness (Geisler et al., 2010) and negative effects of anxiety (Chalmers et al., 2016), sadness (Stange et al., 2017), and anger (Suls, 2013) on HRV. Thus, the reduced phasic vagal activity might be partially accounted for by decreased cheerfulness and increased sadness and anxiety evoked by confrontation with unpleasant and potentially threatening feedback in FA participants. Additionally, the impact of anger possibly caused by the feeling of inaccurate and hurtful judgment may also have overlapped with the aforementioned effects.

It is also important to notice that PSI has been repeatedly linked to depression and anxiety (e.g. Lim et al., 2016; Mahon et al., 2006) which means that its effect on parasympathetic activity observed across studies might be partially fueled by the accompanying negative affect stemming from the PSI. At the same time, the more pronounced effects of manipulation observed in a subgroup of participants who deemed the feedback as accurate suggest that the transient increase in loneliness observed in this group may also have a specific impact on vagal flexibility which cannot be attributed solely to the general increase of the negative affect in participants who received FA feedback. However, while the effects of increased negative emotions cannot be clearly disentangled from the specific impact of loneliness on participants, the pattern of the results observed in the subgroup of the FA participants who believed in the induction suggests that loneliness can have an impact on vagal reactivity that goes over and beyond the general effects of the negative feedback.

The possible causes of the weakened vagal suppression might be understood in the light of previous work on the effects of experimentally induced loneliness. Previous studies using the same experimental paradigm demonstrated that participants in the FA group attended significantly less to negative social pictures (sad, although not angry faces) than other types of stimuli and had an attentional preference for positive social stimuli (DeWall et al., 2009) and that the induction resulted in a reduction of activity in the dorsomedial prefrontal cortex, a region associated with mentalizing processes when observing negative social stimuli (Powers et al., 2013). These effects have been interpreted as indicators of an attempt to disengage from socially derived negative emotions. Similar tendencies were found in lonely (vs non-lonely) young adults who fixate earlier on social threatening stimuli, but also avoided it after the initial exposure (Bangee et al., 2014). This notion was further corroborated by previous studies showing that disengagement and withdrawal in social settings are related to emotional problems in lonely individuals (Coplan et al., 2013; Qualter and Munn, 2002). Thus, in the present study, the decreased vagal suppression of participants in the FA group could be occasioned by an attentional avoidance motivated by the implicit need to blunt continuous negative social stimuli.

The failure to sustain decreased levels of vagal activity during the entire task could also be a result of a transient impairment of self-regulatory capacity necessary for sustained attentional engagement. Multiple studies provided evidence for the adverse impact of loneliness on self-regulation using the experimental paradigm similar to the one used in the current study (Baumeister et al., 2002; Baumeister et al., 2005; Twenge et al., 2007; Twenge et al., 2001; Twenge et al., 2002) and cross-sectional data (DeWall and Pond, 2011; Yusoff et al., 2013; Lauder et al., 2006; Hawkley et al., 2009). Dealing with distress elicited by receiving negative social feedback requires an emotional effort, which in turn consumes cognitive resources necessary for efficient self-regulation (Baumeister et al., 2005) as it constitutes a trade-off between executive functions and emotion suppression on a level of vagal activity (Spangler et al., 2015).

The presented findings corroborate previous correlational work showing that prolonged social problems, such as social anxiety (Movius and Allen, 2005) and trait loneliness (Muhtadie et al., 2015), are related to worse psychophysiological adaptation to demanding events as indexed by weakened vagal suppression. The manipulation used in the study is currently considered the best experimental proxy of long-term condition, and thus the observed effects have a higher potential to overlap with the real-life phenomena (Wirth, 2016). It is of particular importance, given that the psychophysiological consequences of the loneliness induction found in the current study can have a profound impact on one's social well-being and self-regulatory capacity. A meta-analysis of research investigating the relationship between HRV and social skills showed that the lack of cardiac autonomic flexibility reflected by reduction during stressful social situations and recovery afterward could be considered an index of psychopathology (Shahrestani et al., 2015). In another meta-analysis, decreased vagal suppression has been repeatedly related to more externalizing, internalizing, and cognitive problems together with worse social functioning in children from healthy populations (Graziano and Derefinko, 2013). Lack of the ability to continuously regulate vagal activity during the processing of unpleasant social information may thus potentially underlie problems with social engagement, adaptability, and self-control.

Notably, the manipulation did not cause a significant overall increase or decrease in HRV in the FA group but altered its dynamic in response to the task. This finding highlights the importance of using more dynamic psychophysiological measures of sensitivity to social stimuli. While resting vagal tone has been repeatedly shown to be a marker of psychosocial well-being and to influence the ability to react to the social environment adequately (Park et al., 2014; Souza et al., 2007; Kok et al., 2013; Miller et al., 2017; Lischke et al., 2017), task-related changes in vagal activity were shown to be uniquely related to adaptability to stress (Spangler et al., 2018) and trait-loneliness (Muhtadie et al., 2015), effortful control (Sulik et al., 2015), emotion regulation (Zhang et al., 2015) and more adaptive functioning overall (Graziano and Derefinko, 2013).

As noted before, a plethora of psychophysiological research has focused on the relationship between PSI and heightened stress reactions to social situations (Brown et al., 2018). While increased fight-or-flight responses can play a role in the adverse outcome of loneliness, we did not find the manipulation to impact participants' sympathetic activity. In contrast, our findings suggest that loneliness can result in a blunted reaction to and potential disengagement from processing social stimuli. This observation is crucially important in the context of social functioning: the inability to dynamically adapt to demanding situations might be the main obstacle preventing lonely people from engaging in satisfying and meaningful interactions, as social encounters always demand an adjustment to another person's perspective, reappraising ambivalent cues, and occasionally dealing with distressful feedback (Muhtadie et al., 2015). Literature on the effects of loneliness on social cognitive skills has shown that lonely individuals exhibit negative cognitive bias when dealing with social cues, interpersonal interactions and self- and others-related attributions (Spithoven et al., 2017). Thus, the rigidity of psychophysiological response can underlie difficulties in social functioning, but also health implications, as these two were postulated to be tightly related (Kemp et al., 2017). The results demonstrated that even a momentary impression of a lonely life elicited in a controlled environment can have a significant impact on parasympathetic reaction to social stimuli. In line with previous findings, it corroborates the notion that even a transient state of perceived social disconnection, such as migration (Gouin et al., 2015) or forced social distancing (Okruszek et al., 2020) can have a substantial impact on vagal activity, which in turn can hypothetically alter one's adaptability to a dynamic social environment.

While robust, the presented results are limited by several factors. Firstly, we found the experimental groups to differ in their accuracy ratings. The discrepancy comes as no surprise, given previous evidence for a generalized tendency to remain more critical towards undesirable feedback (e.g. Ditto and Lopez, 1992), and it was not significantly correlated with any HRV levels during the task conditions. At the same time, the analysis of participants' affect revealed that the manipulation resulted in increased levels of sadness and anxiety in the FA group as compared with the FB group, and not loneliness itself. The intergroup difference in loneliness could have been found only among participants who perceived the given feedback as mostly accurate. Thus, the hindering effect of manipulation on task-related vagal suppression could have been largely loaded by more general negative affect (which may accompany the feeling of loneliness, but is not its equivalent), although loneliness might have had its own impact on participants who actually found themselves more lonely after the induction. Future studies should address this problem by developing paradigms that allow for a more detailed distinction between the effects of particular negative emotions associated with PSI.

Secondly, the manipulation did not seem to impact explicit ratings of the task stimuli and did not have a differential effect on the task conditions that should produce specific effects of emotion regulation, by either increasing and decreasing affective response to the presented stimuli. Repetitiveness and homogeneity of stimuli might have limited participants' range of responses, which prevented eliciting an emotional reaction strong enough to fully investigate the effects of the experimental induction on reappraisal ability. Importantly, previous studies on hypervigilant attentional patterns in loneliness have provided contradictory results (Bangee et al., 2014; Lodder et al., 2015, Qualter et al., 2013). Therefore, it has been suggested that paradigms based on the static pictures might not be enough to elicit hypervigilance in lonely individuals (Spithoven et al., 2017). The use of the dynamic stimuli, e.g. videoclips containing social stimuli, was thus recommended in social neuroscience research due to its higher ecological validity (Hari et al., 2015).

Thirdly, the study was conducted on the sample of young adults recruited by online advertisements and thus the conclusions cannot be generalized to the entire population. As noted before, young age might be a significant risk factor for loneliness and its long-term consequences, which makes it crucial to examine the effects of PSI in this particular age group. However, future studies should also include more diverse samples in order to identify to what extent changes in age might impact the influence of loneliness on vagal activity. Moreover, while there is little rationale to believe that the fact that most of the participants had secondary or higher education significantly biased the measurement, this factor still should be considered a potential limitation of the current results. As academic achievement was linked to effective emotion regulation in children (Graziano et al., 2007), the fact that most of the participants in the sample obtained higher education might signal increased regulatory capacity of the group as compared to the general population.

Finally, the present examination of psychophysiological consequences of loneliness on the phasic vagal activity should be further complemented by an investigation of underlying neural mechanisms and examination whether these findings may be replicated in ecologically valid data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpsycho.2021.03.002.

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RESEARCH PAPER

Loneliness - not for the faint of heart? Effects of transient loneliness induction on neural and parasympathetic responses to affective stimuli

Marcelina Wiśniewska[a], Aleksandra Piejka[a], Tomasz Wolak[b], Dirk Scheele[c,d] and Łukasz Okruszek[a]

[a]Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Warsaw, Poland; [b]Bioimaging Research Center, World Hearing Center, Institute of Physiology and Pathology of Hearing, Kajetany, Poland; [c]Department of Social Neuroscience, Faculty of Medicine, Ruhr University Bochum, Bochum, Germany; [d]Research Center One Health Ruhr of the University Alliance Ruhr, Ruhr University Bochum, Bochum, Germany

ABSTRACT
While loneliness has been associated with altered neural activity in social brain networks and reduced heart rate variability (HRV) in response to social stressors, it is still unclear whether these are related or parallel effects. Thus, the current study aimed to examine the relationship between loneliness and neural and parasympathetic responses to social stimuli by using an experimental induction of momentary loneliness. Sixty-three participants (18–35 y.o.) received manipulated feedback about their future relationships to induce either loneliness (Future Alone, FA; $n = 31$) or feelings of belonging (Future Belong, FB, $n = 32$) and completed a functional magnetic resonance imaging session with concomitant HRV measurement during which affective pictures with social or nonsocial content were presented. In line with our previous research, decreased vagal flexibility and more negative affect were observed in participants subjected to the loneliness induction. Furthermore, even though no significant between-group differences in neural activity were observed, the neural response to negative social vs nonsocial stimuli in the temporoparietal junction was positively associated with the parasympathetic response, and this relationship was stronger in the FA group. Taken together, these results suggest that transient feelings of loneliness may disrupt adaptive responding to environmental demands and negatively impact brain-heart interactions.

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1. Introduction

Loneliness, defined as a state that occurs when an individual's current social connections are insufficient in relation to their social needs (Hawkley & Cacioppo, 2010), has been repeatedly shown to have negative consequences not only for psychological well-being but also for physical health (Holt-Lunstad et al., 2015). Given the multitude of its negative health sequelae, it is vital to get a better understanding of mechanisms linking psychological and physiological responses in lonely individuals (Hawkley & Cacioppo, 2010; Spithoven et al., 2017). The neurovisceral integration model (NIM) suggests trajectories by which loneliness could produce some of its detrimental physiological effects. NIM posits that ineffective top-down cortical control of the medial prefrontal cortex (mPFC) over the amygdala's automatic responses to unknown stimuli is associated with the decreased capacity to effectively adapt and function in a complex environment (Thayer et al., 2012). Furthermore, the NIM proposes that the mPFC-amygdala interaction could be indexed by heart rate variability (HRV) and thus provides a link to integrate the complex relationship between altered parasympathetic and neural activity. In line with this proposal, greater resting HRV has been associated with adaptive physiological responses to environmental demands and has been linked to more effective emotion regulation ability (Thayer & Lane, 2009), greater self-regulation (Park et al., 2014), and better cognitive functioning (Quintana et al., 2012; Williams et al., 2016). While most of the studies focused on the role of the interplay between prefrontal and subcortical sites, correlational (Chang et al., 2013) and causal data (Miller et al., 2020) point toward involvement of other structure, e.g., temporoparietal junction (TPJ) in neurovisceral regulation.

Importantly, the NIM proposes that inefficient mPFC-amygdala interplay could result in heightened bottom-up threat signaling (Smith et al., 2017), which allows linking it directly with mechanisms postulated by the Evolutionary Theory of Loneliness (ETL). According to the ETL, as social connections are crucial for survival,

CONTACT Łukasz Okruszek lukasz.okruszek@psych.pan.pl Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Jaracza 1, Warsaw 00-378, Poland

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unmet social needs should result in a desire to reconnect with others (Cacioppo & Cacioppo, 2018). However, in lonely individuals, the motivation to approach social stimuli is hindered by avoidance of potential social threats and negative interactions, which increases a focus on self-preservation, and in turn, might lead to further social withdrawal (Cacioppo & Cacioppo, 2018). Furthermore, in line with NIM predictions, loneliness has been linked to decreased parasympathetic regulation, including both decreased resting vagal tone (Roddick & Chen, 2021) and blunted vagal flexibility (Muhtadie et al., 2015). Moreover, mechanisms postulated by the NIM are coherent with patterns observed in neuroimaging studies on lonely individuals. Previous evidence has highlighted the role of several regions associated with the "social brain" structures in relation to loneliness (Lam et al., 2021). Abnormalities of the mPFC in lonely individuals have been shown across different methodologies (Cacioppo et al., 2009; Layden et al., 2017; Nakagawa et al., 2015). Specifically, more pronounced loneliness has been linked to decreased dorsal mPFC (dmPFC) and TPJ responses to social scenes of positive and negative valence, which has been interpreted as evidence for decreased perspective-taking in lonelier individuals (Cacioppo et al., 2009). The role of the amygdala has also been emphasized by findings linking its altered structure (Düzel et al., 2019) and heightened reactivity (Morr et al., 2022) to loneliness, therefore suggesting its impact in altered processing of affective social information in lonely individuals. Moreover, loneliness negatively correlated with regional white matter density in the left TPJ and left dmPFC (Nakagawa et al., 2015), as well as weaker resting-state functional connectivity between the amygdala and prefrontal regions (Layden et al., 2017). These neural alterations may, in turn, exacerbate the effects of loneliness on the misinterpretation of social cues by impairing the functioning of structures involved in top-down regulation processes, such as the mPFC and TPJ.

However, to the best of our knowledge, no previous study examined the association between loneliness, vagal flexibility, and brain activity. Importantly, the investigation of such relationship in individuals with high levels of loneliness could be confounded by numerous factors which may impact both HRV and neural activity in this group (e.g., heightened depression (Gray et al., 2020; Koch et al., 2019; Vanhalst et al., 2012) or social anxiety (Chalmers et al., 2014; Lim et al., 2016)). One way to overcome the issues associated with the cross-sectional investigation of the effects of chronic loneliness is to study trajectories linking neural and parasympathetic responses under experimentally induced transient loneliness, especially given the fact that previous studies have established that both parasympathetic (Piejka et al., 2021) and neural (Powers et al., 2013) responses to social stimuli are susceptible to transient loneliness induction. Piejka et al. (2021) have recently found that being subjected to negative feedback about one's future relationships, which is believed to be the most efficient transient loneliness induction method (Wirth, 2016), reduces one's vagal flexibility in response to facial stimuli. Similarly, decreased dmPFC recruitment in response to negative social scenes was observed after the experimental induction of momentary loneliness (Powers et al., 2013). However, the causal relationship between abnormal brain functioning, vagal flexibility, and momentary loneliness is still unclear.

Therefore, the main aim of the current study is to examine the effects of transient loneliness, induced in a laboratory setting, on neural and parasympathetic responses to affective stimuli. Firstly, we expect to replicate findings from our previous study (Piejka et al., 2021) and observe decreased vagal flexibility in individuals subjected to the induction of loneliness. Vagal flexibility will be defined as a difference between the resting and task-related HRV, hence higher values will indicate a more accurate responding to task-specific demands. Secondly, we hypothesize that, in line with the NIM, decreased vagal flexibility observed in individuals subjected to experimental induction of loneliness will be associated with decreased response in brain regions associated with bottom-up threat signaling (amygdala) and top-down contextualization of such signals (mPFC, TPJ).

2. Methods

2.1. Participants

Sixty-three young (18–35; mean age: 24.52y ± 4.33) right-handed (based on the Edinburgh Handedness Inventory; Veale, 2014) native Polish speakers with no history of psychiatric or neurological disorders, substance abuse, cardiovascular diseases, or MRI contraindications participated in the study. Based on the post-hoc sensitivity analysis (G*Power; version 3.1.9.7), the sample of size $n = 63$ was sufficient to detect a large effect ($f^2 = 0.35$; $1\text{-}\beta = 0.98$). All participants had normal or corrected-to-normal vision. The participants were also screened for depression (dysphoria score < 12, anhedonia score < 8 measured by the Polish version of the revised Center for Epidemiologic Studies Depression Scale (CESD-R; Koziara, 2016)). Furthermore, to decrease the probability of participants not believing in the experimental manipulation, individuals with a degree in psychology were excluded from the study. Given that high (chronic) loneliness has been linked to reduced interpersonal trust (Lieberz et al., 2021), which could affect the credibility of the manipulation and participants with either extremely high or extremely low chronic loneliness scores may not see Future Belong or Future Alone feedback as credible, we recruited participants with a moderate (score range between the 3rd and 8th decile: 32–53; cutoff points were determined based on the data collected from an independent sample of *n* = 923 individuals) level of loneliness, as measured by the Polish version of the Revised UCLA Loneliness Scale (R-UCLA; Kwiatkowska et al., 2017). The study protocol was approved by the Ethical Committee at the Institute of Psychology, Polish Academy of Sciences (application number: 20/XI/2019). Each participant gave informed, written consent and was compensated with 200 PLN for completing the behavioral and fMRI session.

2.2. Procedure

During the first session, participants were invited to the Institute of Psychology, Polish Academy of Sciences, to complete a behavioral assessment. The neuroimaging session took place at the Bioimaging Research Center of the Institute of Physiology and Pathology of Hearing (Kajetany, Poland). Between the sessions, participants also completed a 7-day experience sampling protocol (results reported elsewhere; Piejka et al., 2024).

During the first meeting, participants completed a series of behavioral tasks, filled out a set of self-report questionnaires, and were told, that based on the gathered data, they would receive feedback concerning their social functioning at the consecutive meeting. During the second meeting (see Figure 1), participants undertook two scanning sessions, with the first including functional localizer tasks (see details in section 2.3). At the beginning of the second scanning session, participants were asked to relax while T1-weighted structural images were acquired. Then, the experimental manipulation procedure was applied, and afterward, participants completed the Social-Nonsocial Affective Task (SNAT; see section 2.4).

The experimental manipulation procedure was designed after Twenge et al. (2001). Its first part aimed to make the obtained information seem believable and, therefore, was based on participants' actual Eysenck Personality Questionnaire (EPQ-R; Jaworowska, 2012) scores and consisted of Barnum statements regarding participant's extraversion level. The second part of the feedback was assigned at random and aimed to induce either loneliness (Future Alone, FA) or feelings of belonging (Future Belong, FB) by providing information about participants' future social relationships. Participants in the FA group received information that their

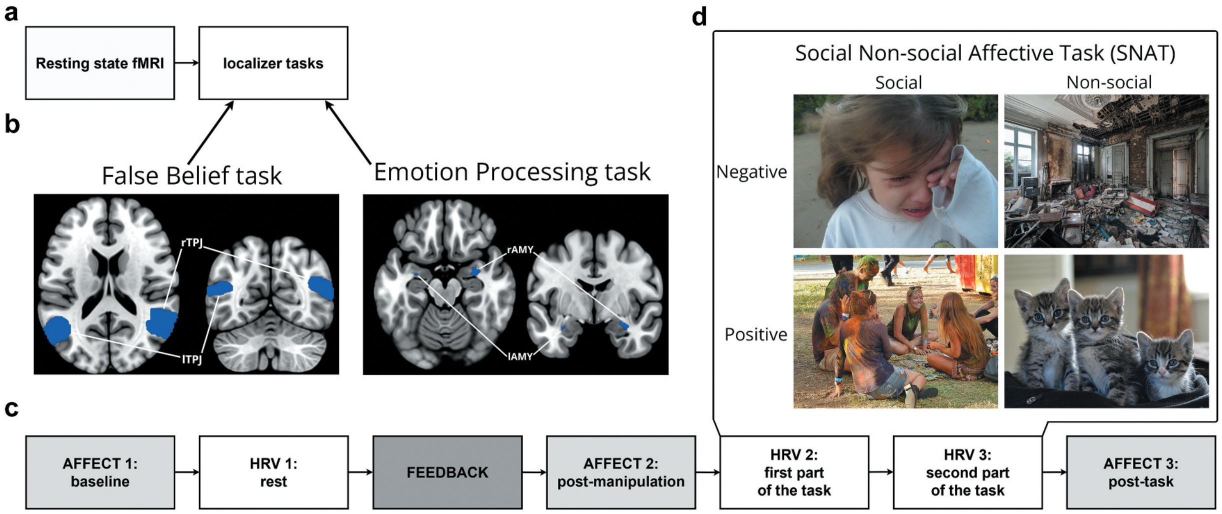

Figure 1. A, The course of the procedure in the first fMRI session (duration: approx. 1 hour). B, ROIs identified by intersecting the False Belief and Emotion Processing tasks with the map from SNAT. C, The course of the experimental induction procedure in the second fMRI session (duration of the entire session: approx. 1 hour). White boxes correspond to 7 min and 20 seconds segments used for HRV analyses; boxes in light gray correspond to self-report affect ratings; the box in dark gray marks the moment of experimental manipulation (duration: 1 min and 35 seconds). D, Example stimuli for each category presented in SNAT. Sample images have not been used in the current study, they were obtained from Flickr under a Creative Commons license (terms can be found at https://creativecommons.org/licenses/by/2.0/). Credits from top left: Mikaela Pelayes (CC BY 2.0), Vincent Ferron (CC BY-NC 2.0), Michael Coghlan (CC BYSA 2.0), Paul Schadler (CC BY 2.0). The images have been converted to CMYK colors, resized and slightly trimmed to reflect the original IAPS proportions, no other changes were made.

relationships will likely not last and they might end up alone later in life. Participants in the FB group were told that they are likely to always have many stable and fulfilling relationships. The exact wording of the feedback can be found in Piejka et al. (2021).

To examine the impact of the induction on their affect, participants were asked to complete a self-report 7-point affect scale consisting of adjectives describing six positive *(joyful, content, happy, cheerful, relaxed, energetic*) and six negative (*tense, irritated, low, worried, lonely, abandoned*) states before the experimental manipulation procedure, right after it, and after SNAT (see Figure 1(c)). Furthermore, at the end of the session, participants were asked whether they considered the feedback presented during the study as accurate using a 7-point Likert scale ranging from 1 - *Definitely not accurate* to 7 - *Definitely accurate*. Upon the completion of the fMRI session, participants were debriefed, and the purpose of the study was explained to them. They were assured that the part of the experimental manipulation concerning their relationships was assigned to them at random and was not based on any of the previously collected data.

2.3. Localizer tasks

The False Belief task (Dodell-Feder et al., 2011) was used to functionally localize the main brain regions of the mentalizing network (mPFC, TPJ). During the task, participants were presented with 10 stories regarding a character's belief about the state of the world (False Belief) and 10 stories describing an outdated state of the world (False Photo) and had to decide whether a statement regarding the story is true or false. The task was presented in two runs and overall lasted 9 minutes and 2 seconds (Golec-Staśkiewicz et al., 2022).

The Emotion Processing task (Barch et al., 2013) was used to functionally localize the amygdala. Participants were presented with blocks of either faces (with angry or fearful expressions; Faces) or geometrical shapes (Shapes) and had to match the target picture displayed on the top of the screen with one of two pictures displayed on the bottom. The task was presented in two runs and overall lasted 5 minutes.

2.4. Social-Nonsocial Affective Task (SNAT)

The stimuli set was composed of 96 pictures from the International Affective Picture System (IAPS; Lang, 2008), 24 for each category (social/nonsocial, positive/negative; see Figure 1(d), full list of the stimuli is available in the Supplementary Materials), chosen in accordance with a previous study which utilized the same experimental manipulation (Powers et al., 2013). During the task, participants were presented with positive and negative pictures depicting either social (defined as the display of a human) or nonsocial content in blocks of 5 pictures (each displayed for 3.2s), separated by a 16-second fixation point. One of the pictures in each block was repeated, and the participant was asked to react with a button press to each repetition (1-back task). The task was presented in four runs, each consisting of six blocks, lasting overall 13 minutes and 20 seconds. The experiment was programmed using NBS Presentation software (Version 20.1).

2.5. MRI data acquisition

The T1-weighted structural images and task-related fMRI images were collected on a 3T Siemens Prisma scanner equipped with a 64-channel head coil. Structural T1-weighted MRI images were acquired with TR = 2400 ms, TE = 2.74 ms, flip angle = 8°, FOV = 256 mm, and with 0.8 mm isotropic voxels. T2-weighted images used to improve pial surface refinement were acquired with TR = 3200 ms, TE = 564 ms, flip angle = 120°, FOV = 256 mm, and with 0.8 mm isotropic voxels. Task-related fMRI images were collected using gradient echo-planar imaging (EPI) sequence with TR = 800 ms, TE = 38 ms, flip angle = 52°, FOV = 216 mm, with 2.0 mm isotropic voxels and multi-band acceleration factor of 8. The numbers of volumes collected for each task were as follows: the False Belief task – 342 volumes, the Emotion Processing task – 188 volumes, SNAT – 250 volumes. To enable distortion correction due to field inhomogeneity, half of the runs of each task was acquired with A-P and half with P-A phase encoding. During the fMRI session, photoplethysmography data (PPG) were recorded using the Siemens scanner pulse oximeter, with the signal sampled at 400 Hz and the sensor placed on the left index finger. Visual stimuli were displayed via the goggle system (NordicNeuroLab VisualSystem HD).

2.6. Data analysis

The analyses of behavioral, physiological, as well as ROI data were performed with JASP (version 0.16.4). Unless stated otherwise, in the analyses, a p-value of less than .05 was considered statistically significant and adjusted for multiple comparisons where applicable, i.e., for post-hoc ANOVA comparisons and multiple correlations. For the latter case, a Bonferroni-corrected threshold for multiple correlations was derived by adjusting p-value by the number of ROIs considered in the correlational analyses (i.e., $p = 0.05/4 = 0.0125$).

2.6.1. *Behavioral analyses*

Positive affect was an average score of the six adjectives describing positive states, and similarly, negative affect was calculated as a mean score for the six items describing negative states. The effects of the experimental manipulation on participants' positive and negative affect were examined by using repeated-measures ANOVAs, with Time (baseline, post-manipulation, post-task) as a within-subject factor and Group (FA, FB) as a between-subject factor and post-hoc test with Bonferroni's correction.

2.6.2. *Physiological data preprocessing and analyses*

The physiological recording data were synchronized with DICOM images, and three 440-second segments were extracted, which corresponded to a time of i) T1-weighted structural images collection (relaxation period, rest), ii) first two runs of SNAT (first part of the task), iii) last two runs of SNAT (second part of the task). The PPG data were pre-processed using Kubios HRV Premium software (version 3.5.0). A smoothness priors detrending ($\lambda = 500$) and the automatic artifact correction with a medium threshold were applied. Upon visual inspection, noisy segments of the data were identified, and potential artifacts were manually removed. For further analysis, a normalized high frequency (HFnu; 0.15–0.40 Hz) power was used as a measure of HRV, representing the relative value of the HF power component compared to the total power, excluding the very-low-frequency (VLF) component, in accordance with guidelines for HRV data analysis (Berntson et al., 1997; Laborde et al., 2017; Malik et al., 1996). Due to equipment malfunction, the PPG data of three participants could not be recovered, and one more participant was excluded due to poor PPG signal quality (more than 5% of artifacts in each segment considered for analyses). Hence, the final sample for the physiological analyses consisted of fifty-nine participants ($N = 59$, 29F; $N_{FA} = 29$, 13F; $N_{FB} = 30$, 16F). The changes in HRV, as measured by mean HFnu values observed during consecutive parts of the procedure, were tested with repeated-measures ANOVA, with Condition (rest, first part of the task, second part of the task) as a within-subject factor and Group (FA, FB) as a between-subject factor. Furthermore, HRV measured during the task was subtracted from HRV measured at rest, to create a vagal flexibility index reflecting changes in parasympathetic response during the procedure.

2.6.3. *Neuroimaging data preprocessing and analyses*

First, distortion correction was performed with FMRIB Software Library's (FSL) topup tool. Then, neuroimaging data were preprocessed using fMRIPrep 23.2.0 (Esteban et al., 2018, 2019) based on Nipype 1.8.6 (Gorgolewski et al., 2011). The full fMRIprep preprocessing boilerplate is available in the Supplementary Materials. Structural T1-weighted images were corrected for intensity non-uniformity with N4BiasFieldCorrection (Tustison et al., 2010), and used as T1-weighted reference. The anatomical image was skull-striped and brain tissue segmentation was performed using FSL's FAST. Spatial normalization to the MNI space was then performed through nonlinear registration with antsRegistration (ANTs 2.5.0). For each of the functional runs, a reference image was generated using custom fMRIPrep methodology and co-registered to the anatomical reference using FreeSurfer's bbregister. Head motion parameters were estimated using FSL's MCFLIRT. The data were then spatially smoothed with a 6 mm full-width-at-half-maximum Gaussian kernel using spm_smooth and further analyzed using Statistical Parametric Mapping (SPM12; Wellcome Trust Centre for Neuroimaging, University College London, UK). Due to the poor quality of the T1-weighted image as assessed by the MRI Quality Control tool (MRIQC; Esteban et al., 2017), one participant was excluded from fMRI analyses. No participants were excluded due to excessive head motion (all movement parameters <3 mm/°), thus leaving the final sample for fMRI analyses of $N = 62$ (31F). For each localizer task and SNAT, a general linear model (GLM), containing onsets and durations of each condition and regressors of no interest estimated during fMRIPrep preprocessing pipeline (six head motion parameters (translation and rotation in x, y, and z dimensions), DVARS, framewise displacement, global signal and six anatomical components (*aCompCor*)), was specified and convolved with a canonical hemodynamic response function (HRF). Maps of the activity of both localizer tasks and SNAT can be found in the Supplementary Materials.

2.6.3.1. ***ROI definition.*** Firstly, in order to spatially constrain search spaces, regions associated with the social brain that showed significantly greater activation in the False Belief task for the Belief > Photo contrast (thresholded at FWE-corrected $p < .05$; $k > 10$) were intersected with the Social > Non-social map obtained from SNAT creating ROIs corresponding to right (rTPJ) and left (lTPJ) TPJ. Secondly, the group activation pattern obtained from the Emotion Processing task (Faces > Shapes contrast) was intersected with the Social > Non-social map from SNAT to create ROIs corresponding to the right (rAMY) and left (lAMY) amygdala (see Table 1 and Figure 1(b)).

Table 1. ROIs defined for analyses.

		Peak coordinates		
ROI	Cluster size	x	y	z
rAMY	48	32	− 6	− 18
lAMY	10	− 32	− 2	− 22
rTPJ	1534	52	− 62	12
lTPJ	831	− 50	− 66	14

rAMY – right amygdala, lAMY – left amygdala, rTPJ – right temporoparietal junction, lTPJ- left temporoparietal junction.

2.6.3.2. ROI analysis. To assess the effects of the experimental manipulation on neural response, the parameter estimates from each ROI for each condition were extracted using the MarsBar toolbox (version 0.44; Brett et al., 2002) and entered into repeated-measures ANOVA with Sociality (Social, Non-Social) and Valence (Positive, Negative) as within-subject factors and Group (FA, FB) as the between-subject factor and post-hoc test with Bonferroni's correction. To investigate the association between ROI activation and parasympathetic response, difference scores for each contrast of interest (negative social > negative nonsocial, positive social > positive nonsocial) were correlated with the vagal flexibility index.

3. Results

3.1. Behavioral results

3.1.1. Positive affect

A main effect of Time was found ($F(2,61) = 3.49$, $p = .03$, $\eta_p^2 = 0.054$), with a lower positive affect post-task (4.08 ± 1.05) than post-manipulation (4.35 ± 1.17; $p = .04$, $d = 0.26$, 95% CI: − 0.01 to 0.54). No main effect of Group ($F(1,61) = 2.41$, $p = .13$, $\eta_p^2 = 0.038$) was observed. However, a significant interaction between the factors was found ($F(2,61) = 9.13$, $p < .001$, $\eta_p^2 = 0.130$), with higher positive affect in the FB group post-manipulation (4.79 ± 1.17) than at baseline (4.31 ± 1.03; $p = .04$, $d = -0.47$, 95% CI: − 0.94 to 0.01) or post-task (3.98 ± 0.99; $p = .002$, $d = 0.60$, 95% CI: 0.12 to 1.09), while no significant differences between affects measured at consecutive timepoints were found within the FA group. The results are shown in Figure 2(a).

A main effect of Group was observed for *relaxed* ($F(1,61) = 6.30$, $p = .015$, $\eta_p^2 = .094$) with participants in the FA group having reported feeling less relaxed than participants in the FB group ($p = .015$). An interaction between Time and Group was found for *joyful*, *content*, and *cheerful* (Fs from 7.70 to 13.40, all ps < .001), with a higher level of each emotion post-manipulation than at baseline or post-task in the FB group, and lower in the FA group. Detailed results from the analysis of individual items can be found in the Supplementary materials.

3.1.2. Negative affect

There were no significant effects of Time ($F(2,61) = 0.52$, $p = .60$, $\eta_p^2 = 0.008$) or Group ($F(1,61) = 0.006$, $p = .94$, $\eta_p^2 < 0.001$). However, we observed an interaction between

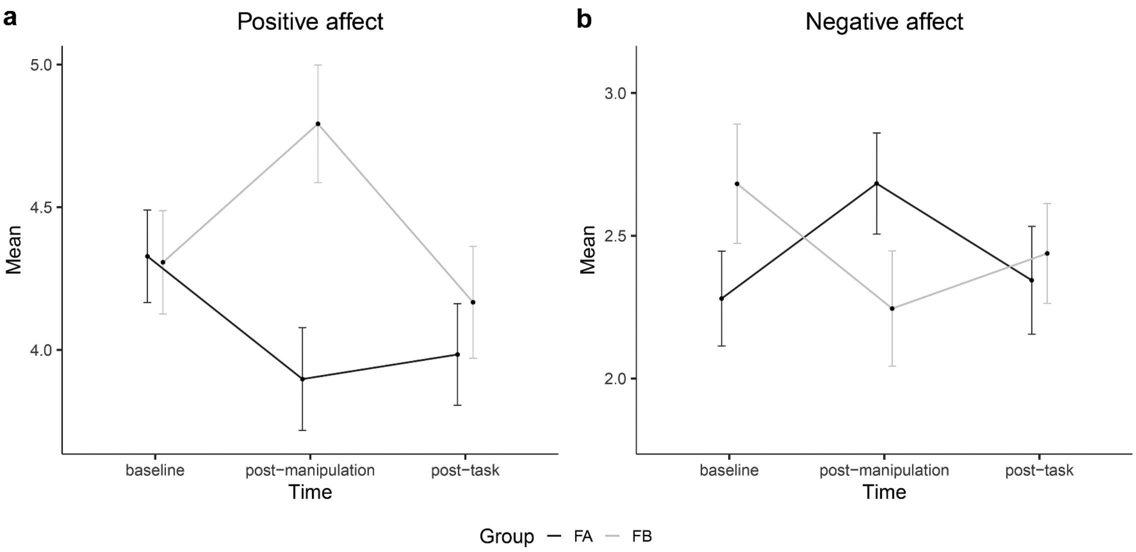

Figure 2. Mean self-ratings of positive (a) and negative (b) affect during the procedure in the FA and FB group
Note. FA - Future Alone, FB - Future Belong group; error bars indicate standard error of the mean

the factors (F(2,61) = 10.18, $p < .001$, $\eta_p^2 = 0.143$). In the FA group, negative affect post-manipulation (2.68 ± 0.99) was significantly higher than at baseline (2.28 ± 0.92; $p < .05$, d = – 0.38, 95% CI: – 0.80 to – 0.001), while in the FB group, negative affect was lower post-manipulation (2.24 ± 1.14) than at baseline (2.68 ± 1.18; $p = .02$, d = 0.42, 95% CI: 0.04 to 0.83). No other significant differences were found. The results are shown in Figure 2(b).

Investigation of specific items revealed interactions between Time and Group for *tense*, *worried*, *irritated*, and *low* (Fs from 4.29 to 7.69, all ps < .02). The participants in the FB group reported a lower level of tension, worry, and feeling low post-manipulation compared to baseline or post-task measure. In contrast, the participants in the FA group reported having felt more worried, irritated and low post-manipulation than at baseline or post-task. No significant effects for *lonely* or *abandoned* were found. A detailed description of the observed effects from the analysis of individual items can be found in the Supplementary materials.

3.1.3. Manipulation check

Due to an omission error, the ratings of the feedback's accuracy were not collected in the first batch of participants and could only be analyzed for a subset of participants ($n = 58$). The mean overall feedback was rated as less accurate by the participants in the FA group (4.76 ± 1.35) than the participants in the FB group (5.93 ± 0.92; t(56) = – 3.85, $p < .001$, d = – 1.01, 95% CI: – 1.78 to – 0.56). While there was no significant difference in ratings regarding the part of the feedback based on the EPQ-R score (t(56) = – 1.22, $p = .23$, d = – 0.32, 95% CI: – 1.00 to 0.25), the FA group considered the received information concerning their future relationships as less accurate than the FB group (FA = 3.86 ± 1.57, FB = 5.24 ± 1.12; t(56) = – 3.84, $p < .001$, d = – 1.01, 95% CI: – 2.10 to – 0.66).

3.2. Heart rate variability

A main effect of Condition was observed (F(2,57) = 5.25, $p = .007$, $\eta_p^2 = 0.84$), with HFnu, which reflects the parasympathetic activity during the procedure, being significantly lower during the second part of the task (46.43 ± 14.42) than at rest (49.97 ± 13.25; $p = .007$, d = 0.243, 95% CI: 0.83 to 6.15). No significant effect of Group was observed (F(1,57) = 0.45, $p = .50$, $\eta_p^2 = 0.008$). However, there was a significant interaction between Condition and Group (F(2,57) = 5.47, $p = .005$, $\eta_p^2 = 0.88$). In the FB group, HFnu during the second part of the task (43.86 ± 13.91) was significantly lower than at rest (50.81 ± 13.94; $p < .001$, d = 0.48, 95% CI: 2.35 to 11.56), while no similar changes were found in the FA group, indicating decreased vagal flexibility as a result of the induction of loneliness. Based on these results, for each participant, a vagal flexibility index was calculated by subtracting HRV corresponding to the second part of the task from HRV at rest. The results are shown in Figure 3.

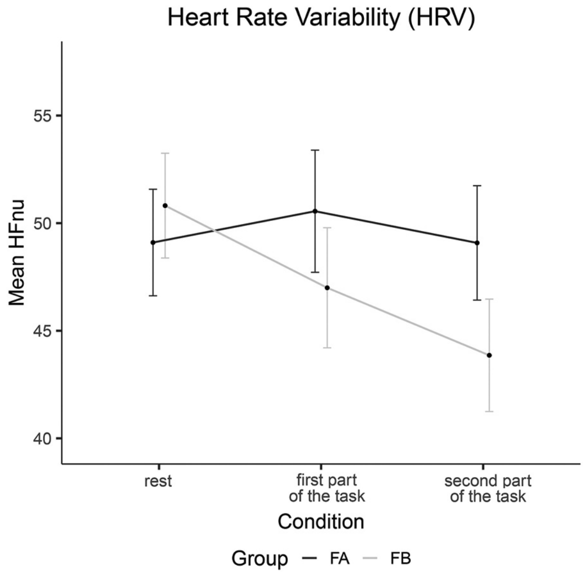

Figure 3. Mean HRV across conditions in the FA and FB group Note. FA - Future Alone, FB - Future Belong group; error bars indicate standard error of the mean

3.3. fMRI results

3.3.1. Task effects and ROI activation

Across all participants, the comparison of Social versus Non-social conditions, irrelevant of valence, revealed significant clusters of brain activity in the social perception network consisting of the bilateral fusiform face area (FFA) and the bilateral extrastriate body area (EBA), as well as the network associated with mentalizing including bilateral TPJ, temporal pole and precuneus, and emotion processing network including the amygdala (see details in Table S3 and Figure S4 of the Supplementary Materials). No significant cluster of activation was found in the mPFC for the Social > Non-social contrast, hence, it was not considered in further analysis. Exploratory whole-brain analysis ($p < .05$ FWE cluster-corrected) of between-group differences revealed increased activation of a region encompassing Crus I of the left cerebellar hemisphere for participants in the FB compared to those in the FA group across all conditions, as well as for the social and positive condition. Compared to the FB group, participants in the FA

Table 2. Zero-order correlations between vagal flexibility index and ROIs activation

Contrast	negative social > negative nonsocial contrast			positive social > positive nonsocial contrast		
Group ROI	all participants	FA Group	FB Group	all participants	FA Group	FB Group
rAMY	0.016	0.181	− 0.134	− 0.083	− 0.214	0.055
lAMY	0.012	0.204	− 0.059	− 0.150	− 0.039	− 0.154
rTPJ	0.222	0.307	0.181	0.011	0.033	0.077
lTPJ	0.334*	0.492**	0.214	− 0.161	− 0.128	− 0.077

FA – Future Alone, FB – Future Belong group; * - *p* < .05, ** - *p* < .01.

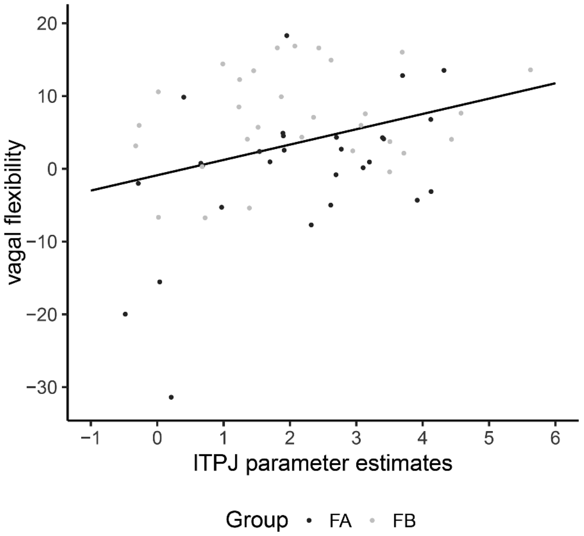

Figure 4. Association between activation of lTPJ for negative social > negative nonsocial contrast and vagal flexibility index across all participants
Note. FA - Future Alone, FB - Future Belong group

group demonstrated increased activation of structures of the visual cortex, i.e., calcarine fissure and cuneus across all conditions (please see section 2.6 in the Supplementary Materials for detailed tables with peak coordinates).

Viewing social scenes in comparison to nonsocial scenes was associated with greater activation for each ROI considered for analyses (rAMY, lAMY, rTPJ, lTPJ; Fs from 29.58 to 239.37, all ps < .001). A main effect of Valence was observed for each ROI except for rTPJ (Fs from 7.16 to 24.79, all ps < .05), with rAMY, lAMY and lTPJ displaying greater activation for negative when compared to positive scenes. Neither a significant effect of Group nor an interaction between Group and other factors was found for any of the ROIs. An interaction between Sociality and Valence was found for rAMY, lAMY and rTPJ (Fs from 4.42 to 4.59, all ps < .05). A detailed description of the observed effects can be found in the Supplementary materials.

3.3.2. Associations between ROI activation and vagal flexibility

Zero-order correlations between ROI activation and vagal flexibility are presented in Table 2. Across all participants, a significant correlation between vagal flexibility and activation in response to negative social compared to negative nonsocial stimuli was found only for the left TPJ (r(56) = 0.334, *p* = .010; see Figure 4). Further investigation of this effect in each group revealed that the association between vagal flexibility and lTPJ activation was significant in the FA group (r(26) = 0.492, *p* = .008), but not in the FB group (r(28) = 0.214, *p* = .255), however the difference between the correlation coefficients did not reach statistical significance (z = 1.2; *p* = .24). No association between vagal flexibility and activation of any other ROI was found.

4. Discussion

The current study aimed to investigate the impact of a transient loneliness induction on neural and parasympathetic responses to affective stimuli. Firstly, the effectiveness of the experimental manipulation was indicated by the changes in affect ratings observed in each group during the procedure. The negative affect increased in the FA group after the loneliness induction while in the FB group, a reverse pattern was found. Additionally, the positive affect was significantly higher after having obtained feedback regarding one’s future relationships only in the FB group.

Secondly, the FA intervention significantly impacted parasympathetic markers, an effect which was not found in the FB group. This pattern is congruent with findings from our previous study (Piejka et al., 2021), in which the loneliness induction resulted in blunted vagal withdrawal in response to social content. As change in HRV from rest to task indicates an adjusted response to environmental challenges (Muhtadie et al., 2015; Park et al., 2014; Weber et al., 2010; Wei et al., 2024) and was found to be negatively correlated with loneliness (Muhtadie et al., 2015), the results of the current study suggest that the loneliness induction disrupted adaptive physiological responding to task demands.

Importantly, further investigation into specific affect ratings revealed higher levels of feeling low, irritated and worried in the FA group and lower level of tension, worry, and feeling low in the FB group, with no significant differences in the level of reported loneliness during the procedure. Possibly, participants in the FA group experienced negative affective states, which may produce similar effects on the parasympathetic level as momentary loneliness. Indeed, decreased vagal reactivity has been previously linked to increased depressive (Schiweck et al., 2019) and anxiety (Levine et al., 2016) symptomatology, as well as a nonspecific general stress response (Kim et al., 2018). Thus, the decreased parasympathetic regulation observed in the FA group may be partially attributed to the generalized mood effects of the induction rather than evoked feelings of loneliness per se. A similar pattern of results was found in our previous study, which also utilized the Future Alone paradigm (Piejka et al., 2021). The effects of reported feelings of loneliness were only evident after taking into consideration the subset of participants who perceived the obtained feedback as accurate. However, in the current study, similar analyses could not be reliably repeated due to sample size being less than half of that in the previous study.

Moreover, we also observed widespread involvement of social brain networks in response to social vs nonsocial stimuli presented during the tasks. All of the regions of interest of the “social brain” investigated in the current study have shown sensitivity to social compared to nonsocial content, and negative social stimuli elicited higher response in regions associated with automatic response to salient environmental stressors (bilateral amygdala) and top-down mentalizing processes (bilateral TPJ). While each of these regions was selected using independent localizers, to ensure the interpretation of results with regard to social cognitive processes, no significant between-group differences in their activity in response to social vs nonsocial stimuli were observed. This result contradicts previous findings from a study that utilized the same induction method and stimuli set (Powers et al., 2013). In the study by Powers et al. (2013), reduced activity of dmPFC for negative social relative to negative nonsocial scenes was found in individuals subjected to the FA induction. In the current study, however, the examination of task effects did not reveal significant clusters of activation in mPFC which would allow for between-group comparison of its recruitment when viewing social scenes. Furthermore, while links between loneliness and hypervigilance to social threats are postulated by the Evolutionary Theory of Loneliness (Cacioppo & Cacioppo, 2018), no increased activity of regions associated with bottom-up affective response was found in participants subjected to the loneliness induction in the current study. However, it may be noted that previous studies based on the IAPS stimuli also failed to find increased activity of the amygdala in high-lonely individuals (D’Agostino et al., 2019; Wong et al., 2016). Thus, the use of more dynamic social stimuli instead of static pictures could more accurately resemble naturalistic social situations.

While this study focused on differences in the neural response of a priori-defined regions, an exploratory investigation of whole-brain effects revealed clusters of activation in the cerebellum that were linked to greater activity in the FB than in the FA group. As the cerebellum’s role in affective processing has been previously emphasized (Pierce et al., 2023), its increased involvement could indicate emotion-relevant processing of particularly social and positive content in participants in the FB condition. In contrast, in comparison to the FB group, participants subjected to the loneliness induction demonstrated increased activation of structures associated with the visual cortex, which is a finding comparable to the results reported by Cacioppo et al. (2009). However, in the current study, the effect was not specific to any particular task condition but rather may indicate more general preferential processing of visual stimuli at earlier stages of the processing pathway following the loneliness induction.

A positive coupling between the parasympathetic response and activation of the left TPJ for negative social in comparison to negative nonsocial scenes was observed in the current study. The TPJ is believed to constitute the core node of the mentalizing network, as making inferences about others’ beliefs has been associated with the consistent engagement of bilateral TPJ (Molenberghs et al., 2016; Schurz et al., 2021). However, the distinction between the roles of the right and left TPJ has also been previously emphasized in belief-processing (Arioli et al., 2023), as well as in salience and attention networks (Kucyi et al., 2012), with rTPJ engaged in reorienting attention toward unexpected salient stimuli in the social context (Schuwerk et al., 2017) and with lTPJ demonstrating sensitivity to the contextually-relevant semantic content (Guterstam et al., 2021). Furthermore, the role of TPJ in adjusting physiological response to cognitive demands has been previously suggested based on resting-state functional connectivity data (Chang et al., 2013). In the study by Miller et al. (2020) the inhibition of right TPJ through transcranial magnetic stimulation (TMS) resulted in decreased vagal withdrawal during the emotion induction procedure in which, following the TMS administration, participants were asked to watch a neutral and a sad film clip and provide their affect and empathy ratings. Participants who received inhibitory TMS over the TPJ also reported increased feelings of irritation and were less likely to feel concern for others over empathetic sadness compared to the control group who received TMS over the vertex (Miller et al., 2020), thus indicating not only altered psychophysiological but also affective responding after disrupting TPJ activity. Therefore, the relationship between the TPJ activation and parasympathetic response in the current study might be reflective of adjusting physiological response in order to attend to task-specific demands. As repeated exposure to negatively-valenced social content could have resulted in arising feelings of uneasiness in the current study, it can be hypothesized that the association between parasympathetic response and TPJ activation is indicative of the increased need to regulate the emotional discomfort in our participants. In line with this assumption, the role of the left TPJ has been previously demonstrated in the empathic processing of emotions (Kogler et al., 2020), as well as in regulating emotions of others and reducing feelings of emotional distress (Guendelman et al., 2022). Hence, the observed pattern of neural and parasympathetic activation might be indicative of self-regulatory processes that occurred to adjust the affective response and facilitate attendance to task requirements. While the seminal study by Cacioppo et al. (2009) has found decreased involvement of the temporoparietal regions in response to negative social vs nonsocial stimuli, the current study has not found significant between group differences in task-related TPJ activations. This difference may stem from the fact that while both studies included participants with low-to-average chronic loneliness levels, Cacioppo et al.'s study has compared patterns of brain activity in participants median-splitted with regard to the chronic loneliness score, while in the current study FA and FB participants did not differ with regard to chronic loneliness levels to avoid confounding manipulation induction effects. Importantly, the association between vagal flexibility and the left TPJ activity was more than twice as strong in FA group participants compared to those in the FB group, which may be tentatively interpreted as a compensatory effect in FA participants. This notion is corroborated by previous evidence, which demonstrated stronger connectivity between lTPJ compared to the rTPJ and the executive control network (Kucyi et al., 2012). In the context of the current study, this might thus further suggest that a stronger association between parasympathetic response and lTPJ activation indicates initial compensatory top-down regulation of affective social content in response to FA feedback. A similar link between loneliness and cognitive control networks has previously been demonstrated for trait-like loneliness (Wong et al., 2022). Hence the current results may extend this notion to momentary loneliness. Still, as the difference in the relationship strength did not reach statistical significance, further investigations with larger samples are needed, as the sample size in the current study was not sufficient to detect medium or small effects.

Several limitations of the current study can be pointed out. Firstly, the manipulation procedure did not influence specific feelings of loneliness, but rather elicited nonspecific negative affect. The observed effects of experimental manipulation might have been limited by the fact that participants in the FA condition perceived the obtained feedback as less accurate than participants in the FB group. Nonetheless, receiving preference-inconsistent information has been repeatedly found to be examined more critically (Ditto & Lopez, 1992), and perceiving the negative feedback as less accurate did not change the effects of the loneliness induction on the physiological level (Piejka et al., 2021). Additional insight could be offered by implementing a more complex procedure of loneliness induction which focuses on participants' recall of past experiences of loneliness (Roddick & Chen, 2021), and thus could resemble the subjective experience of chronic loneliness more accurately. Several methodological factors can also be addressed in future studies – firstly, the current task did not include neutral stimuli, which limited the comparisons between conditions and did not allow for the investigation of the linear effects of valence, which may also explain the difference with regard to studies which based their investigation on negative vs neutral contrasts (e.g., Cacioppo et al., 2009). Similarly, due to the financial constraints we could not examine more populous samples which would allow detecting small to moderate effects, nor add a nonsocial control condition, which has been proposed by Twenge et al. (2001), i.e., future misfortune condition. However, importantly, the validity of the misfortune control condition has been questioned (Wirth, 2016), as reliving the experience of social pain may be less difficult than reliving the physical pain. Thus, instead of creating three undersampled subgroups, we decided to focus on FA vs FB conditions only. Furthermore, while PPG is considered sufficient for reliable HRV measurement, it is also more susceptible to motion artifacts (Schäfer & Vagedes, 2013), hence, its use instead of ECG resulted in lower signal accuracy. Similarly, the block task-design which has been utilized in the current study prevents investigation of the effects which may be present at the single trial level and evidenced by coupling between neural response to specific stimuli and short-term heart rate acceleration. Given the fact that emotion regulation is a dynamic process, averaging moment-to-moment processes involved in the regulation of the response toward social stimuli may have obscured the association between brain activity and psychological and physiological processes observed in participants.

Nevertheless, the results of the current study offer insight into mechanisms evoked by the experimental induction of loneliness and indicate that trajectories linking loneliness and brain-heart interaction are more complex than posited by the ETL. However, more investigation is needed to determine whether the same mechanisms are affected when chronic loneliness is considered. Furthermore, as the experimental manipulation was conducted in a controlled laboratory setting in the current study, the generalizability of the findings should be tested by investigating the physiological mechanisms elicited by momentary loneliness using more ecologically-valid methods.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data and code for the study will be uploaded before the end of the project (30 April 2025) to the https://osf.io/ecgb2/.

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Original Article

Distinct fusiform subregion activity and connectivity in lonely and nonlonely individuals during social information processing

Marcelina Wiśniewska[1], Aleksandra Piejka[1], Tomasz Wolak[2], and Łukasz Okruszek[1,*]

[1]Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Jaracza 1, 00-378 Warsaw, Poland
[2]Bioimaging Research Center, World Hearing Center, Institute of Physiology and Pathology of Hearing, Mokra 17, Kajetany, 05-830 Nadarzyn, Poland
[*]Corresponding author: Łukasz Okruszek, Social Neuroscience Lab, Institute of Psychology, Polish Academy of Sciences, Jaracza 1, 00-378 Warsaw, Poland.
Email: lukasz.okruszek@psych.pan.pl

Loneliness has been recognized as a major public health concern affecting individuals' everyday social functioning. Although hypothesized, the association between chronic loneliness, neural responses, and parasympathetic regulation during social information processing remains underexplored. This study aimed to compare parasympathetic and neural responses to affective social content in well-powered samples of participants with different chronic loneliness levels. In this study, 104 (52 females) healthy young adults were recruited based on their chronic loneliness levels to form groups of lonely and nonlonely individuals. Participants underwent a functional magnetic resonance imaging session in which they passively viewed social and nonsocial images of negative, positive, and neutral valence. Both groups showed similar task-related vagal changes and responses across predefined regions associated with key social brain areas. However, an exploratory whole-brain activity analysis revealed between-group differences in two distinct fusiform face area subregions. Furthermore, the lonely individuals group showed decreased connectivity between one of the fusiform face area subregions and right temporoparietal junction compared to the nonlonely individuals group. These results suggest that trait-like loneliness is associated with distinct processing of social content in fusiform face area subregions, potentially linking loneliness to differences in effective social information integration.

Keywords: fMRI; fusiform face area; heart rate variability; loneliness.

Introduction

Loneliness is defined as a distressing experience that arises when the quantity and quality of one's social relationships are perceived as insufficient to meet social needs (Perlman and Peplau 1981). Chronic loneliness is associated with adverse physical health outcomes (Holt-Lunstad et al. 2015) and mental health problems (Mann et al. 2022). Studies on the biological mechanisms through which loneliness may impact long-term health have primarily focused on sympathetic nervous system functioning (Brown et al. 2018), particularly stress reactivity (Nowland et al. 2018). However, increasing evidence also suggests that loneliness affects parasympathetic function, particularly heart rate variability (HRV) (Xia and Li 2018). An important theoretical framework explaining these effects is the neurovisceral integration model, which proposes that HRV reflects cortical inhibition of automatic responses to unknown stimuli and thus serves as an indicator of the capacity of an organism to adapt and function effectively under environmental stressors (Thayer and Lane 2000). Importantly, adaptive physiological responding depends on both vagal tone measured at rest and dynamic changes in vagal control as a response to situational context. Greater HRV at rest has been linked to better abilities associated with social cognition (Quintana et al. 2012), and the use of adaptive emotion regulation strategies and flexible emotional responding (Balzarotti et al. 2017). Moreover, individuals demonstrating greater vagal withdrawal (ie a decrease in parasympathetic activity) from resting state to task engagement, followed by swift recovery to baseline levels after task completion, may process social information more effectively and show enhanced sensitivity to social contexts (Thayer et al. 2012). This phenomenon reflects the ability to rapidly redirect metabolic resources from homeostatic maintenance toward environmental engagement. Such resource reallocation enables adjustment of sensory processing thresholds and increases sensitivity to subtle social and emotional cues (Muhtadie et al. 2015). Thus, rigid negative reactions and difficulties with self-regulation during social interactions in lonely individuals (LIs) could be linked to inefficient parasympathetic responses. It could also be hypothesized that different loneliness levels might have differential effects on specific aspects of vagal regulation. For example, acute feelings of loneliness altering phasic, rapid changes in parasympathetic response, while chronic loneliness is associated with more general markers of poor vagal regulation, such as reduced vagal tone at rest.

Expanding on this notion, our previous study demonstrated the impact of induced loneliness on self-reported affective and parasympathetic responses during social information processing (Piejka et al. 2021). Participants in the study received bogus feedback based on the personality test results that led them to anticipate either a future filled with satisfying relationships or a

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lonely life. We found that participants subjected to momentary loneliness induction demonstrated a blunted pattern of vagal regulation while responding to social information compared to those subjected to social belonging induction. Specifically, after the belonging induction, a decrease in HRV occurred from rest to task completion followed by post-task recovery, which marks an adaptive physiological response to the task demands. In contrast, in the lonely group, HRV differed from the baseline only at the task's onset, but not during its subsequent stages.

A similar pattern of the parasympathetic response, suggesting that momentary loneliness may disrupt adaptive physiological reactions to social cues, was observed in our subsequent neuroimaging study (Wiśniewska et al. 2025). Furthermore, we extended the previous findings by showing an association between vagal withdrawal and task-related activation of the left temporoparietal junction (TPJ). The relationship between left TPJ task-related activation and vagal withdrawal was stronger in participants subjected to loneliness induction than in those subjected to the induction of social belonging. This suggests a link between momentary loneliness and the initiation of self-regulatory processes in response to affective social content. This notion is further supported by the results of another study using a similar design, which found decreased recruitment of the medial prefrontal cortex (mPFC) in response to negative social stimuli in individuals subjected to loneliness induction (Powers et al. 2013). Importantly, the role of the mPFC in influencing brain-HRV interactions has been emphasized by the neurovisceral integration model (Thayer et al. 2012). Higher HRV has been associated with stronger functional connectivity between the mPFC and subcortical structures (Sakaki et al. 2016), and with mPFC connectivity within the default mode and salience networks (Jennings et al. 2016), therefore corroborating the association between parasympathetic response and neural mechanisms underlying efficient responding to context-specific cognitive demands (Smith et al. 2017). However, several findings also indicated the importance of involvement of the TPJ in integrating neural and parasympathetic responses (Chang et al. 2013; Miller et al. 2020). Moreover, positive links between both mPFC and TPJ activation and higher task HRV have been associated with the use of adaptive emotion regulation strategies (Guendelman et al. 2024); therefore, the emotional responding in LIs could be linked to affected interactions between HRV changes and the social brain network.

Importantly, previous studies have documented both synergistic (Tomova et al. 2020) and opposing (Archer Lee et al. 2022) effects of momentary and chronic loneliness on behavioral and neural activity associated with social functioning. Thus, it remains uncertain whether the patterns of neural and parasympathetic responses elicited by the transient induction of momentary loneliness in our previous studies can also be observed in chronically LIs. Although we have previously observed blunted task-related vagal regulation as a result of momentary loneliness induction (Piejka et al. 2021; Wiśniewska et al. 2025), we found no direct relationship between chronic loneliness and resting vagal tone in a large, sex-balanced sample of healthy young adults (Piejka et al. 2024a). No association between chronic loneliness and resting HRV has been reported in other studies (Hawkley et al. 2006; Muhtadie et al. 2015). In contrast, other studies have provided evidence of a link between chronic loneliness and both lower resting HRV (Gouin et al. 2015; Roddick and Chen 2021) and decreased HRV reactivity (Roddick and Chen 2021; Song et al. 2025). Therefore, the relationship between chronic loneliness and parasympathetic responses remains unclear.

Similarly, the patterns of brain activity observed across neuroimaging studies on momentary and chronic loneliness are inconsistent. Chronic loneliness is theorized to be linked to heightened bottom-up threat signaling toward social stimuli (Hawkley and Cacioppo 2010). However, previous studies reported no significant links between momentary (Wiśniewska et al. 2025) or chronic loneliness (D'Agostino et al. 2019) and amygdala (AMY) response to socioaffective stimuli. Nonetheless, evidence of AMY structural abnormalities in chronically LIs (Lam et al. 2021) and abnormal connectivity patterns (Layden et al. 2017; Tian et al. 2017) has been reported. Given the role of AMY in social cognitive processes (Edmonds et al. 2024), loneliness may be linked to abnormal activation and coupling between the cognitive control and emotion processing networks, rather than solely to the abnormal involvement of the latter during socioaffective processing (Wong et al. 2022).

This notion may be particularly important given the crucial role of mPFC-AMY coupling in interpreting novel and potentially threatening environmental stimuli (Tottenham 2015). The ability to overcome automatic threat responses in such cases is attributed to the top-down effect of the mPFC over automatic bottom-up AMY responses (Smith et al. 2017). Consistent with previous observations of reduced mPFC activity in experimentally induced loneliness (Powers et al. 2013), several studies have consistently demonstrated an association between chronic loneliness and abnormalities in structural integrity (Nakagawa et al. 2015; Kiesow et al. 2020) and task-related functioning (Courtney and Meyer 2019) of the mPFC. As the mPFC is considered crucial for mentalizing processes (Schurz et al. 2020), its reduced activation might affect the ability of LIs to understand others' perspectives, particularly in accounting for the situational context while mentalizing (Hartwright et al. 2012). Further support for the role of abnormal coupling between the mPFC and other brain structures also stems from studies showing that default mode network connectivity differentiates LIs from nonlonely individuals (NLIs) (Spreng et al. 2020), and this connectivity may be used to predict loneliness scores (Feng et al. 2019; Geng et al. 2025).

As highlighted by previous studies (Geng et al. 2025), the TPJ, whose activity correlated with reduced vagal withdrawal in our experimental study (Wiśniewska et al. 2025), may play an important role in understanding the mechanisms of social cognition associated with loneliness. The TPJ functional connotations encompass attentional control (Kucyi et al. 2012), social information integration (Wu et al. 2015), and mentalization (Schurz et al. 2020). Thus, the inefficient functioning of the TPJ in LIs could lead to disturbances at different levels of social information processing, possibly affecting both attention to social cues and the interpretation of such stimuli. Prolonged misperceiving of social interactions could, in turn, intensify feelings of loneliness. Indeed, results from previous functional neuroimaging studies have indicated reduced activation toward unpleasant social versus nonsocial stimuli in the TPJ (Cacioppo et al. 2009), which has been interpreted as reflecting decreased perspective-taking abilities in lonelier individuals. Notably, these conclusions were drawn from relatively small samples with a constrained loneliness distribution. Furthermore, the functional lateralization of the TPJ may further disambiguate whether chronic loneliness affects the integration of sensory and contextual social information involving the right TPJ (rTPJ; Jakobs et al. 2012) or social-semantic content supported by the left TPJ (lTPJ; Zhang et al. 2023).

This study aimed to compare parasympathetic and neural responses to affective social content in well-powered samples of participants with different chronic loneliness levels. Consistent with our previous study (Wiśniewska et al. 2025), we investigated the pattern of HRV changes during the procedure in relation to the activity of the main social brain networks. In order to target functionally distinct regions and to allow an interpretation of the results in relation to social cognitive processes, our analysis focused on predefined regions of interest (ROIs) associated with bottom-up (AMY) and top-down (mPFC/TPJ) social cognitive processes. As the use of independent localizers reduces the number of multiple comparisons and increases the statistical sensitivity in the analyses (Saxe et al. 2006), the study included completion of 2 robust functional localizer tasks. With the false belief localizer (Dodell-Feder et al. 2011), it was possible to delineate functional regions involved in theory of mind and therefore to examine activity of mPFC and bilateral TPJ during socioaffective processing. Even though AMY is a well-defined anatomical region, the use of the emotion processing localizer (Hariri et al. 2002) allowed us to examine the activation of a region associated with processing of threatening facial stimuli, hence potentially enabling the investigation of social threat signaling in association with loneliness. In line with our preregistered hypotheses, we expected to observe reduced activity of TPJ and mPFC, as well as reduced functional connectivity between AMY and social brain structures (TPJ/mPFC) in LIs compared to NLIs during social information processing. In addition, we explored associations between HRV and social brain activity, expecting decreased pattern of vagal flexibility to be associated with decreased activity of mPFC and TPJ in LIs compared to NLIs. Furthermore, we explored the pattern of activity to social compared to nonsocial stimuli in LIs and NLIs by performing exploratory whole-brain analysis.

Materials and methods

Participants

One hundred and four (52 females [F]) participants aged 18 to 35 (23.92 ± 4.16 yr) were recruited from the top (LIs; $n = 52$, 26F) and bottom (NLIs; $n = 52$, 26F) quartile of the Polish version of the Revised UCLA Loneliness Scale (Kwiatkowska et al. 2017) distribution. Based on the data from previous projects ($n = 1{,}899$, individuals aged 18 to 35 yr), cutoff points of 32 (NLI; loneliness score range from 21 to 32; 28.52 ± 2.82) and 49 (LI; loneliness score range from 49 to 73; 56.71 ± 5.50) were determined (the data can be found at https://osf.io/ecgb2/). A power analysis, calculated using the pwr package in R software, indicated that a sample of 52 participants per group allows detecting medium between-group effects at $P = 0.05$ with 71% power. The groups did not differ in age ($t(102) = 0.42$, $P = 0.67$) or years of education ($t(102) = -0.28$, $P = 0.78$). All participants were right-handed (based on the Edinburgh Handedness Inventory; Veale 2014), native Polish speakers with normal or corrected-to-normal vision, and had no contraindications for magnetic resonance imaging (MRI) or electroencephalography (EEG). Participants were screened for neurological and psychiatric disorders, substance abuse, and cardiovascular disorders. In addition, participants with dysphoria score ≥ 12 or anhedonia score ≥ 8 on the Polish version of the revised Center for Epidemiologic Studies Depression Scale (Koziara 2016) or a body mass index > 30 were excluded. All participants provided written informed consent before participating in the study and were reimbursed 100 PLN (~25 USD) for completing the functional MRI (fMRI) session. The study protocol was approved by the Ethical Committee at the Institute of Psychology, Polish Academy of Sciences (application number: 21/XI/2019).

Procedure

The study was preregistered (https://osf.io/vqp8r), and while the scope of this study focuses on neuroimaging data, it was part of a project that included 3 laboratory sessions (behavioral, fMRI, and EEG sessions) and a 7-day experience sampling protocol (for details of the latter, please see Piejka et al. 2024b). Neuroimaging data were collected using a 3T Siemens Prisma scanner with a 64-channel head coil at the Bioimaging Research Center of the Institute of Physiology and Pathology of Hearing (Kajetany, Poland). The session included functional (see details in sections Social-nonsocial affective task (SNAT) and Localizer tasks) and structural data acquisition. At the beginning of the scanning session, before structural T1-weighted image acquisition, participants were asked to rate how accurate each positive ("joyful," "content," "happy," "cheerful," "relaxed," and "energetic") and negative ("tense," "irritated," "low," "worried," "lonely," and "abandoned") adjective describes their current affect on a 7-point scale (ranging from 1 ["definitely not"] to 7 ["definitely yes"]). Cardiac responses were recorded during the procedure using a photoplethysmography (PPG) scanner pulse oximeter, with the sensor placed on the left index finger.

Social-nonsocial affective task (SNAT)

A total of 144 pictures were selected from the International Affective Picture System (IAPS; Lang 2008), with 24 stimuli per content (social/nonsocial) and valence (positive/neutral/negative) category. Stimuli selection was performed based on a previous study investigating the effects of the experimental induction of loneliness (Powers et al. 2013). The brightness of 8 pictures from the set was adjusted to balance the luminance ($F(5,138) = 1.09$, $P = 0.366$, $\eta_p^2 = 0.038$) and contrast ($F(5,138) = 1.35$, $P = 0.246$, $\eta_p^2 = 0.047$) across categories. A complete list of the stimuli used in this study is available in the Supplementary Materials. During the task, participants were presented with blocks of 5 images, each depicting either social or nonsocial content with positive, neutral, and negative valence. The stimulus trial duration was set to 3.2 s, with each image displayed for 3 s. The blocks were separated by a 16-s fixation cross-presentation. To ensure sustained attention during the procedure, one of the pictures in each block was repeated, and participants were asked to react with a button press (one-back task). The task was presented in 4 5-min runs, each consisting of 9 blocks. The task was programmed using the NBS Presentation software (Version 20.1). A sample trial of the task is shown in Fig. 1.

Localizer tasks

To define ROI associated with top-down mentalizing and bottom-up emotional responses, 2 independent localizer tasks were presented during the scanning session. In the first task, the false belief localizer (Dodell-Feder et al. 2011), participants were presented with 10 short stories in which a character had a false belief about the state of the world and 10 stories portraying an outdated state of the world. Each story was displayed for 10 s, and participants were asked to read it and assess whether a short statement displayed afterward (4 s) was true or false. The task was presented in 2 runs, each lasting 4.5 min. In the second task, the emotion processing localizer (Hariri et al. 2002), participants were presented with blocks containing either faces (with either angry or fearful expressions) or geometrical shapes. They were asked to decide whether the picture on the right or left side of the bottom of the screen matched the target picture on the top of the screen. The task was presented in 2 2.5-min runs.

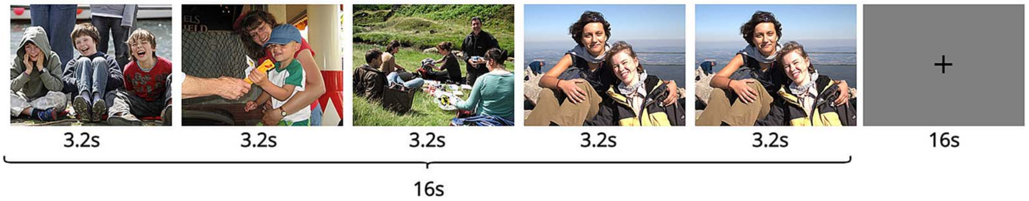

Fig. 1. Sample trial of positive social block in SNAT. The pictures presented were not used in this study; the list of stimuli from the IAPS is available in the Supplementary materials. Images were obtained from Flickr under the creative commons license (https://creativecommons.org/licenses/by/2.0/). Credits from left: Alan cleaver (CC BY 2.0), tom Caswell (CC BY 2.0), Tim Herrick (CC BY 2.0), and Chris Wilson (CC BY-NC-ND 2.0). The images were resized and trimmed to reflect the original IAPS proportions; no other changes were made.

MRI data acquisition

Structural images were acquired with a T1-weighted 3D MP-RAGE protocol with the following parameters: repetition time (TR) = 2,400 ms, echo time (TE) = 2.74 ms, flip angle = 8°, field of view (FOV) = 256 mm, and 0.8 mm isotropic voxels. T2-weighted images were collected with TR = 3,200 ms, TE = 564 ms, flip angle = 120°, FOV = 256 mm, and 0.8 mm isotropic voxels. Functional data were acquired using a Multi-band gradient echo-planar imaging (EPI) sequence with TR = 800 ms, TE = 38 ms, flip angle = 52°, FOV = 216 mm, 2.0 mm isotropic voxels, and a multi-band acceleration factor of 8. For each run of the SNAT, false belief task, and emotion processing task, 374, 342, and 188 volumes, respectively, were collected. Half of the runs of the task-related fMRI were collected with anterior-to-posterior phase encoding and the other half with posterior-to-anterior phase encoding to enable distortion correction for magnetic field inhomogeneities. Visual stimuli were displayed with the NordicNeuroLab Visual System HD Google system, and eye-movement data were collected using the ViewPoint EyeTracker pupil-tracking system (Arrington Research, Inc.). PPG data were recorded using a Siemens scanner pulse oximeter sampled at 400 Hz.

Data analysis

Behavioral and physiological data preprocessing and analyses

The mean positive and negative affect scores, along with individual items from both scales, were tested using 2-sample t-tests to assess between-group differences at the start of the procedure.

Following a pre-existing protocol from our previous study (Wiśniewska et al. 2025), the PPG recordings were synchronized with DICOM images, and 3 440-second segments were extracted, which corresponded to (i) T1-weighted structural image collection (rest), (ii) the first 2 runs of SNAT (first part of the task), and (iii) the 2 consecutive runs of SNAT (second part of the task). The PPG data were pre-processed and analyzed using the Kubios HRV Premium software (version 3.5.0). Data were detrended using a smoothness priors approach ($\lambda = 500$), and the automatic artifact correction with a medium threshold was applied. Noisy data segments were identified through visual inspection, and any potential artifacts were manually removed. An estimate of normalized high frequency (HFnu; 0.15 to 0.40 Hz) power was extracted and used as a measure of HRV in further analyses, consistent with guidelines for HRV data analysis (Berntson et al. 1997; Laborde et al. 2017). Owing to equipment malfunction, the PPG data of 3 participants could not be recovered, and an additional 11 participants were excluded because of poor PPG signal quality (>5% artifacts in any of the 3 segments considered for analyses). Hence, the final sample for physiological analyses consisted of 90 participants (43F, $n_{LI} = 45$, $n_{NLI} = 45$). Changes in HRV, assessed via mean HFnu values across consecutive parts of the procedure, were tested using repeated-measures analysis of variance (ANOVA), with condition (rest, first part of the task, second part of the task) as a within-subject factor, and group (LI, NLI) as a between-subject factor.

Neuroimaging data preprocessing and analyses

The differences between the preregistered plan and the current manuscript regarding the choice of software for the fMRI data analysis are detailed in Table S1 in the Supplementary Materials. After distortion correction, performed using FMRIB Software Library's (FSL) top-up tool, neuroimaging data were preprocessed using fMRIPrep 23.2.0 (Esteban et al. 2018, 2019) based on Nipype 1.8.6 (Gorgolewski et al. 2011). Structural T1-weighted images were corrected for intensity nonuniformity with N4BiasFieldCorrection (Tustison et al. 2010) and used as the T1-weighted reference. The anatomical image was skull-striped, and brain tissue segmentation was performed using FSL's FAST. Spatial normalization to the Montreal Neurological Institute space was performed using nonlinear registration with antsRegistration (ANTs 2.5.0). For each functional run, a reference image was generated using the custom fMRIPrep methodology and co-registered with the anatomical reference using FreeSurfer's bbregister. Head motion parameters were estimated using the FSL's MCFLIRT. The fMRIprep preprocessing boilerplate is available in the Supplementary Materials. Data were spatially smoothed with a 6 mm full-width-at-half-maximum Gaussian kernel using spm_smooth and further analyzed using Statistical Parametric Mapping (SPM12; Wellcome Trust Centre for Neuroimaging, University College London, UK). Owing to excessive head motion during SNAT ($n = 3$) and the false belief localizer ($n = 1$), as indexed by the standardized DVARS parameter evaluated by the MRI Quality Control tool (Esteban et al. 2017), 4 participants were excluded from further analyses. Thus, the final sample for neuroimaging analysis consisted of 100 participants (48F; $n_{LI} = 48$, $n_{NLI} = 52$).

For each participant, a general linear model (GLM) was developed, incorporating the onsets and durations of the 6 SNAT conditions and regressors of no interest estimated during the fMRIPrep preprocessing pipeline. The regressors included 6 head motion parameters (translation and rotation in the x, y, and z dimensions), DVARS, framewise displacement, and 6 anatomical components (aCompCor). Moreover, as the role of global signal in physiological noise contribution has been previously emphasized (Falahpour et al. 2013), and its use as a subject-specific confound has been demonstrated to be effective at denoising motion when used with CompCor's regressors (Parkes et al. 2018), it was also included as a regressor. The model was convolved with a canonical hemodynamic response function. To obtain activation maps of both localizer tasks and SNAT, allowing us to define ROIs we performed

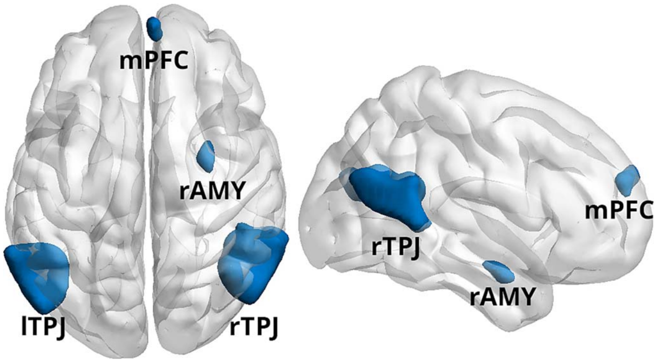

Fig. 2. ROI selected for analyses. ROI, region of interest; rTPJ, right temporoparietal junction; lTPJ, left temporoparietal junction; mPFC, medial prefrontal cortex; rAMY, right amygdala.

Table 1. MNI coordinates of each ROI selected for analyses.

ROI	Cluster size	Peak coordinates		
		x	*y*	*z*
rTPJ	2,018	52	−62	10
lTPJ	1,088	−50	−72	16
mPFC	112	4	64	28
rAMY	121	28	−2	−20

ROI, region of interest; rTPJ, right temporoparietal junction; lTPJ, left temporoparietal junction; mPFC, medial prefrontal cortex; rAMY, right amygdala; MNI, Montreal Neurological Institute.

a second-level full-factorial analysis, including the conditions of each task (false belief task: belief, photo; emotion processing task: faces, shapes; SNAT: 3 levels of valence [negative, positive, and neutral], and 2 levels of content [social and nonsocial]).

ROI analyses

The group activation map from the false belief task (belief > photo contrast; see details in Fig. S5 and Table S5 in the Supplementary Materials) was intersected with the social > nonsocial pattern obtained from the SNAT to define ROIs corresponding to the rTPJ, lTPJ, and mPFC. Similarly, the group activation pattern from the emotion processing task (faces > shapes contrast; see details in Fig. S6 and Table S6 in the Supplementary Materials) was intersected with the social > nonsocial map from the SNAT to create an ROI corresponding to the right amygdala (rAMY) (see Fig. 2 and Table 1). As no significant cluster of activation was observed in the left AMY for the social > nonsocial contrast, it was not considered in further analyses. Using the MarsBar toolbox (Brett et al. 2002), parameter estimates from each ROI were extracted from the first-level models for each participant and entered into a repeated-measures ANOVA with sociality (social and nonsocial) and valence (negative, positive, and neutral) as within-subject factors, and group (LI and NLI) as the between-subject factor. Bonferroni correction was applied for multiple comparisons.

Connectivity analysis

Connectivity analyses were performed using the CONN toolbox (version 21). To investigate the differences in task-related functional connectivity patterns of the main nodes of the social network between the LI and NLI groups, we conducted an ROI-to-ROI generalized psychophysiological interaction (gPPI) analysis for the contrasts of interest (social > nonsocial, negative social > negative nonsocial, positive social > positive nonsocial, and neutral social > neutral nonsocial). All pre-defined ROIs (rTPJ, lTPJ, mPFC, and rAMY) were included as seeds in the analysis.

Exploratory analyses

We also investigated differences in neural activation between groups during the SNAT using a 3 × 2 × 2 full-factorial GLM, incorporating 3 levels of valence (negative, positive, and neutral), 2 levels of content (social and nonsocial), and group as the between-subject variable (LI and NLI). Furthermore, clusters of activation exceeding the cluster-level correction threshold were entered as seeds for exploratory gPPI analysis.

Results

Affect ratings

The mean negative self-reported affect at the beginning of the scanning session was higher in the LI group (3.40 ± 1.16) than in the NLI group (1.85 ± 0.70; $t(98) = 8.14$, $P < 0.001$). Conversely, the mean positive affect was lower for LI (3.68 ± 1.06) than for NLI (4.85 ± 1.14; $t(98) = -5.29$, $P < 0.001$). The same pattern was significant for each item on the negative ($ps < 0.001$) and positive ($ps \leq 0.005$) affect scales.

HRV

A significant main effect of condition was observed ($F(2,88) = 50.20$, $P < 0.001$, $\eta_p^2 = 0.363$), with HFnu being significantly higher during rest (mean$_{\text{HFnu}}$ 53.83 ± 16.48) than during the first (46.77 ± 15.54; $P < 0.001$, $d = 0.437$, 95% CI: 4.53 to 9.59) and second parts of the task (43.58 ± 16.34; $P < 0.001$, $d = 0.634$, 95% CI: 7.72 to 12.78). Moreover, HFnu during the second part of the task was lower than during the first part ($P = 0.008$, $d = 0.197$, 95% CI: 0.66 to 5.72; see Fig. 3). No significant effect of group ($F(1,88) = 0.44$, $P = 0.51$, $\eta_p^2 = 0.005$), or condition *x* group interaction ($F(2,88) = 0.49$, $P = 0.49$, $\eta_p^2 = 0.008$) was observed.

Neuroimaging results

Across all participants, the processing of social versus nonsocial stimuli revealed significant clusters of brain activity in the social

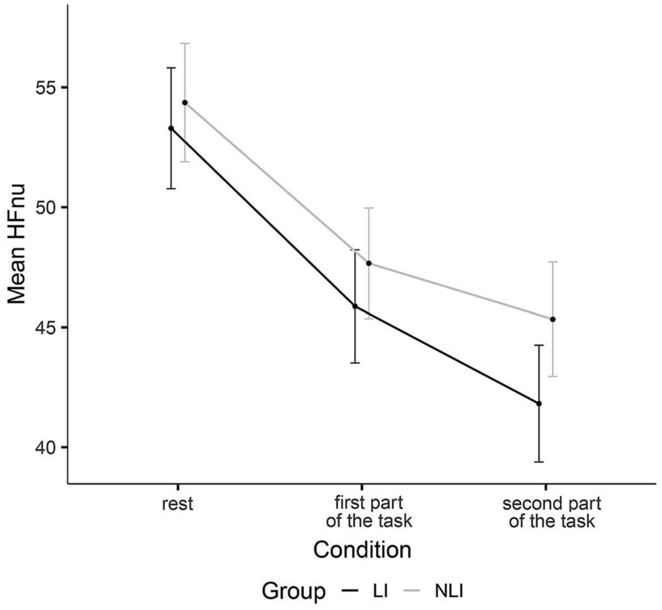

Fig. 3. Mean HRV across conditions during the procedure for all participants. Error bars indicate the standard error of the mean; LIs, lonely individuals, NLIs, nonlonely individuals.

perception network, including the bilateral FFA; emotion processing network, including the rAMY; and mentalizing network, including the mPFC, precuneus, and temporal regions corresponding to the bilateral TPJ, right superior temporal sulcus, and right temporal pole. Overlapping activation patterns were observed for specific contrasts of interest (see Figs S1 to S4 and Tables S2 to S5 in the Supplementary Materials for detailed task effects).

ROI analyses

In all ROIs (rTPJ, lTPJ, mPFC, and rAMY), significant effects of sociality (Fs = 26.94 to 358.23, all ps < 0.001, $\eta_p{}^2 = 0.216$ to 0.785) and valence (Fs = 30.32 to 75.03, all ps < 0.001, $\eta_p{}^2 = 0.236$ to 0.434) were observed. For all ROIs, viewing social scenes was associated with greater activation than viewing nonsocial scenes. Similarly, viewing negative scenes was linked to greater activation than viewing positive or neutral scenes. In addition, viewing positive scenes was associated with greater lTPJ ($P = 0.037$) and mPFC ($P < 0.001$) activation than viewing neutral scenes. A significant interaction between sociality and valence was observed for rAMY ($F(2,98) = 4.77$, $P = 0.009$, $\eta_p{}^2 = 0.046$), which displayed greater activation for viewing negative social scenes than other conditions (all ps < 0.001). No main effect of group or interaction between group and sociality or valence was observed. Moreover, no significant correlation was observed between the activation of the ROIs and changes in HRV during the procedure.

Connectivity analysis

No significant between-group differences in ROI-to-ROI connectivity were observed for any contrast of interest.

Exploratory analysis

The exploratory whole-brain analysis of social versus nonsocial conditions for the LI > NLI contrast (cluster-based family-wise error (FWE) correction, $k = 171$) revealed a cluster of brain activation in the right FFA (36, −62, −16), corresponding to the mid-lateral fusiform gyrus (mFus; Rosenke et al. 2021). Similarly, comparing social versus nonsocial conditions for the NLI > LI contrast (cluster-based FWE correction, $k = 129$) revealed a cluster of brain activation in the right FFA (44, −74, −8) corresponding to the posterior lateral fusiform gyrus (pFus; Rosenke et al. 2021); see details in Fig. 4 and Table 2). Further investigation of task-related functional connectivity using mFus and pFus as seed regions revealed decreased connectivity between mFus and the right temporal region corresponding to the rTPJ (peak at [60, −54, 30]) for the social > nonsocial contrast in the LI > NLI comparison (see Fig. 5 and Table 3).

Discussion

This study aimed to investigate the physiological mechanisms associated with trait loneliness by comparing task-related neural and parasympathetic responses during social information processing between LIs and NLIs. We observed changes in HRV during the procedure and the sensitivity of predefined ROIs to the task conditions. However, the observed between-group differences did not converge with the predicted pattern in our hypotheses.

Consistent with our previous findings (Piejka et al. 2021; Wiśniewska et al. 2025), we observed a significant change in HRV between the rest and task conditions across all participants. This pattern of parasympathetic response has also been consistently reported in other studies using similar procedure designs (Park et al. 2014; Hilgarter et al. 2021; Magnon et al. 2022) and is indicated to reflect attendance to the cognitive demands of the task. Our previous findings demonstrated a blunted vagal response resulting from momentary loneliness. However, in this study, no differences in parasympathetic response were observed between chronically lonely and nonlonely participants. Importantly, despite our previous findings indicating the impact of loneliness induction on brain–heart interactions (Wiśniewska et al. 2025), associations between ROI activation and changes in HRV were also not found in this study. These findings suggest that although momentary feelings of loneliness might induce momentary stress responses and impact parasympathetic regulation and its association to neural response during social information processing, these effects cannot be generalized to groups that differ in trait loneliness. Nevertheless, our previous findings suggest that the relationship between chronic loneliness and resting vagal tone may be moderated by sex and mediated

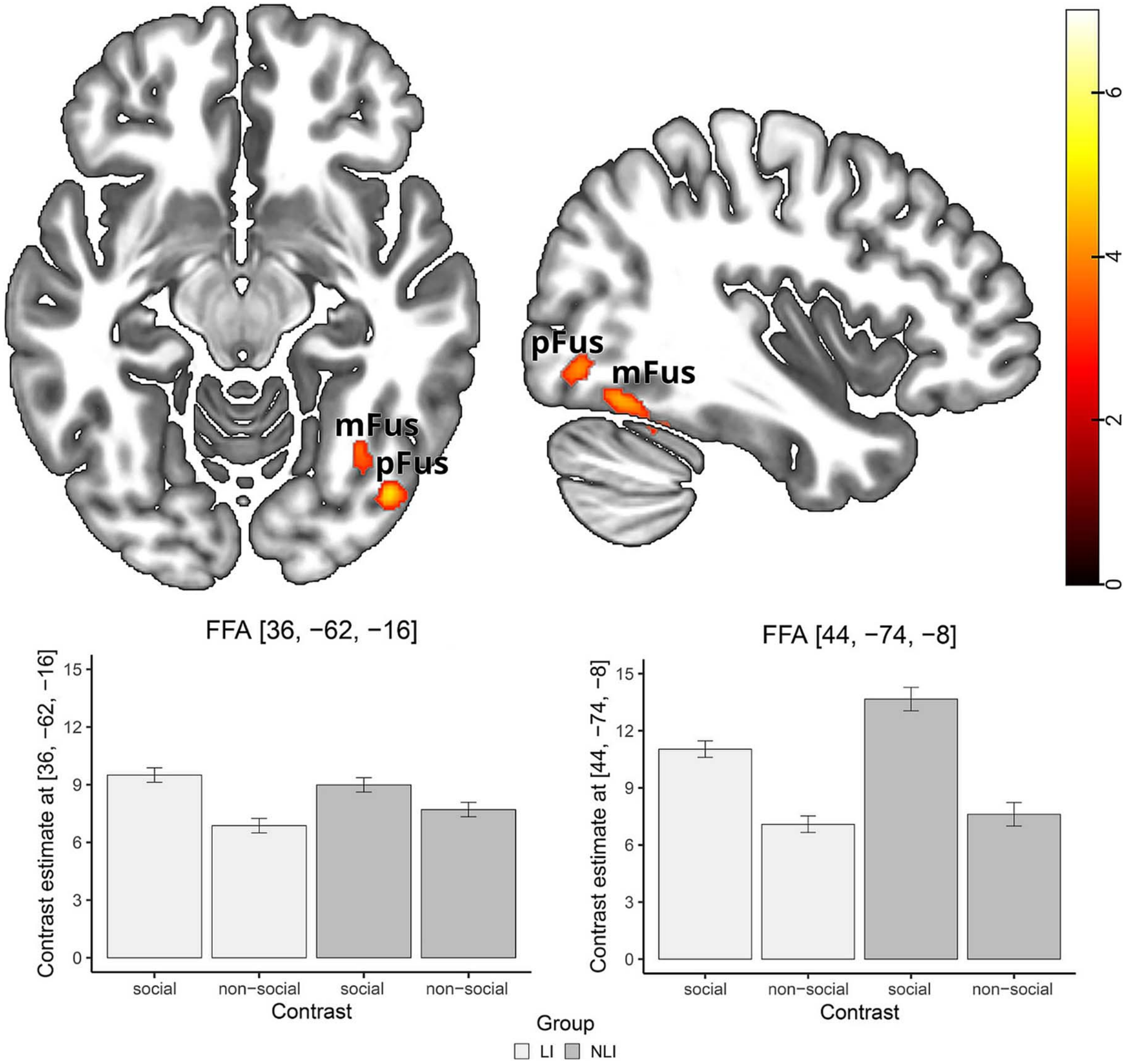

Fig. 4. Between-group differences for the social > nonsocial contrast of SNAT. SNAT, social-nonsocial affective task; FFA, fusiform face area; mFus, mid-lateral fusiform; pFus, posterior lateral fusiform gyrus.

Table 2. FFA clusters.

Contrast	Region	Cluster size	Peak coordinates			T-value
			x	y	z	
LI > NLI	mFus	171	36	−62	−16	5.29
NLI > LI	pFus	129	44	−74	−8	5.99

LIs, lonely individuals; NLIs, nonlonely individuals; FFA, fusiform face area; mFus, mid-lateral fusiform; pFus, posterior lateral fusiform gyrus.

by depressive symptomatology (Piejka et al. 2024a), potentially obscuring between-group differences in this study.

A robust pattern of activation to task conditions was found in all analyzed ROIs across all participants. However, contrary to our predictions, no between-group differences in activation of pre-defined "social brain" ROIs were observed. While a lack of association between chronic loneliness and activation of AMY is in line with previous findings (D'Agostino et al. 2019), these results contradict prior evidence linking loneliness to altered task-related activation of TPJ (Cacioppo et al. 2009), and mPFC (Courtney and Meyer 2019). Consistent with the existing literature, the rAMY showed increased activation in response to negative social scenes compared to the remaining conditions. Abnormal AMY activity and connectivity, both at rest and during socioaffective processing (Duval et al. 2015; Kleshchova et al. 2019), have been linked to abnormal threat vigilance in anxiety-related disorders. Thus, the increased reactivity of these structures toward negative social stimuli could be indicative of previously postulated hypervigilance toward social threats in loneliness (Hawkley and Cacioppo 2010). Despite these suggestions, no between-group differences in rAMY responses to socioaffective stimuli were observed in this study. Moreover, we did not observe reduced task-related functional connectivity between the AMY and cortical structures associated with top-down regulation in LIs versus NLIs during this task. Importantly, no significant cluster of activation was observed in the left AMY for the comparison of social to nonsocial condition, hence this region was not considered in further analyses. While right AMY activation has been linked to automatic detection of emotional faces, the activation of left AMY has been associated with a more sustained

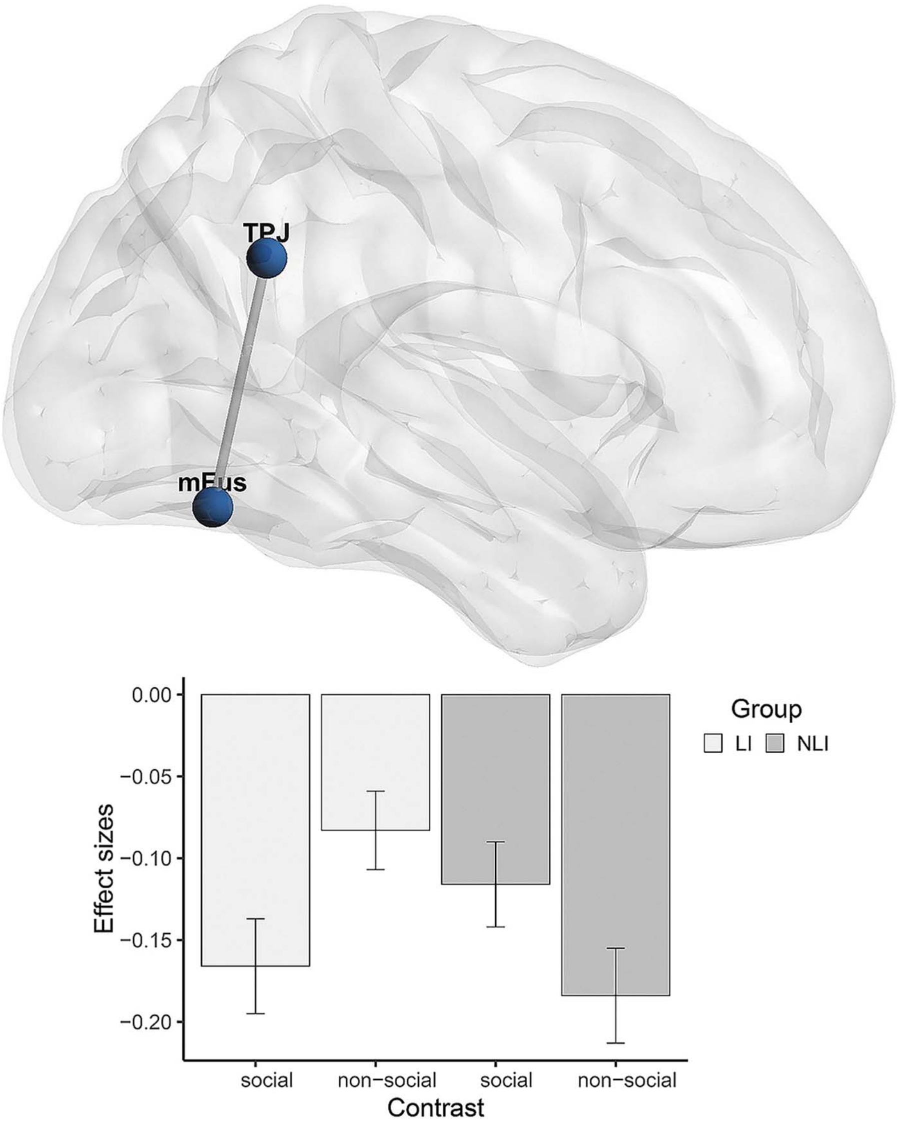

Fig. 5. Seed-to-voxel connectivity results between FFA [mFus; peak at 36, −62, −16] and TPJ [peak at 60, −54, 30]. FFA, fusiform face area; TPJ, temporoparietal junction; mFus, mid-lateral fusiform.

response to emotional stimuli (Dahlén et al. 2022), hence in the current study the lack of significant left AMY involvement could be attributed to the main task used in the procedure which did not require increased engagement in emotions of presented characters.

Similarly, no between-group differences in neural activation were observed in the main nodes of the theory of mind network, namely, the bilateral TPJ and mPFC. Importantly, the lack of between-group effects linked to the chronic loneliness levels in this study contrasts with previous results showing the impact of experimentally induced momentary loneliness on the activity of these regions (Powers et al. 2013; Wiśniewska et al. 2025). The use of a false feedback procedure to induce loneliness may produce momentary effects on self-referential (mPFC) and perspective-taking (TPJ) processes. However, such effects may not be present in chronically LIs when faced with a passive viewing task without explicit instructions associated with mental state attribution, as in this study. Therefore, the design of the experimental task may have limited the ability to draw conclusions regarding the higher-order processing of social information associated with mental state attribution in the participants.

Additional insight into the differences in affective processing observed in LIss and NLI in this study was gained by comparing the whole-brain patterns of activation between the groups. We observed a different pattern of response to social versus nonsocial content in 2 clusters of the FFA. Although the FFA is a well-defined face-selective region (McGugin and Gauthier 2016), it is also associated with responsiveness to more general social stimuli (Schurz et al. 2020). Different subregions of the FFA exhibit distinct patterns of connectivity (Chen et al. 2023) and functional associations (Caspers et al. 2014). Notably, the mFus, which showed an increased response to social stimuli in LIs compared to NLIs, has been considered a "transitional area between early and higher visual cortex" (Caspers et al. 2014). Thus, at earlier stages of the processing pathway, lonelier individuals display more preferential processing of social over nonsocial visual stimuli. In turn, the pFus showed increased activation in response to social stimuli in LIs than NLIs. As pFus is considered a higher-order area, the involvement of the right pFus has been associated with a more pronounced role in face perception and increased activation during affective processing, instead of visual language processing, which has been linked to the left pFus activation (Caspers et al. 2014).

Table 3. Seed-to-voxel connectivity results for LI > NLI group for social > nonsocial contrast, thresholded at $P < 0.001$ with FWE-cluster correction at $P < 0.05$.

Seed region	Region	Cluster size	Peak coordinates			T-value
			x	y	z	
FFA [36, −62, −16]	Angular gyrus	106	60	−54	30	3.39

FFA, fusiform face area; FWE, family-wise error.

Thus, contrary to our predictions, the decreased pFus responses observed in LIs may potentially link higher trait loneliness to less pronounced engagement in affective social content.

Investigation of functional connectivity during the task further enhanced our understanding of the obtained results. An exploration of connectivity patterns with the mFus and pFus as seed regions demonstrated decreased connectivity between the mFus and right TPJ for LIs during social compared to nonsocial conditions. Considering the role of mFus in processing early social stimulus characteristics and the involvement of TPJ in mental state processing (Golec-Staśkiewicz et al. 2022), this relation could potentially link loneliness to less efficient integration of contextual social information (Jakobs et al. 2012). Thus, in LIs, ineffective integration of perceptual and contextual information could result in an inadequate perception of others, potentially impacting adaptive responses during social interactions. Nevertheless, the observed effects should be further investigated in a more naturalistic context. Notably, no hypothesized between-group differences in connectivity between the predefined ROIs were observed.

Conclusion

Similar patterns of HRV changes during the procedure and task-specific activation of the regions associated with the social brain network were observed in both LIs and NLIs. However, we found different activity and connectivity patterns of two fusiform face area subregions, suggesting links between chronic loneliness and effective social information integration. Although this study encompassed a large prestratified sample and employed a standard affective picture-viewing task, some limitations should be acknowledged. The use of static images in the main task of the procedure may have limited the ability to capture more nuanced differences in social cue processing between LIs and NLIs. Therefore, future studies should implement tasks with more naturalistic stimuli to reflect complex social information and examine possible differences in mental state attribution linked to trait loneliness. Moreover, in this study, PPG was used to measure the changes in HRV during the procedure. Considering the susceptibility of PPG to motion artifacts (Schäfer and Vagedes 2013), its use led to the exclusion of a subset of participants from the analysis. Finally, the effects observed in the study could be complemented by examining the temporal dynamics of social affective information processing in relation to loneliness, for example, using EEG event-related potentials (Mąka et al. 2025).

Author contributions

Marcelina Wiśniewska (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Visualization, Writing—original draft, Writing—review & editing), Aleksandra Piejka (Data curation, Formal analysis, Investigation, Writing—review & editing), Tomasz Wolak (Methodology, Resources, Writing—review & editing), and Łukasz Okruszek (Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Writing—review & editing).

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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