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Automaticity of attention capture and engagement: the role of semantic congruency and emotional relevance

Ph.D. thesis
Completed in the Laboratory of Brain Imaging
of the Nencki Institute of Experimental Biology
Polish Academy of Sciences

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Warsaw, 2024

This research was funded by the National Science Centre Poland (Grants No. 2018/29/B/HS6/02152 and 2019/33/B/HS6/02233 awarded to Dr. Michał Bola, Ph.D., D.Sc.).

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Abbreviations

DP - dot-probe task

EEG - electroencephalography

EPN - early posterior negativity

ERP - event-related potentials

IAPS - International Affective Picture System

ID - identification task

N2pc - N2 posterior contralateral

NAPS - Nencki Affective Picture System

NCC - neural correlates of consciousness

QD - quartile deviation

RT - reaction time

RPT - Recurrent Processing Theory

SDT - Signal Detection Theory

SPCN - sustained posterior contralateral negativity

V1 - visual area 1

VAN - Visual Awareness Negativity

Streszczenie

Ilość informacji zmysłowych, które napływają z naszego otoczenia przekracza możliwości ich skutecznego przetworzenia przez mechanizmy percepcyjne i poznawcze. Dlatego nawigowanie w codziennych sytuacjach wymaga mechanizmu selekcji, który wybiera treści najbardziej istotne dla naszego funkcjonowania. Tę właśnie rolę przypisuje się mechanizmowi selektywnej uwagi. W badaniach eksperymentalnych uwaga jest najczęściej badana przy pomocy uproszczonych, sztucznie wygenerowanych bodźców, tak więc czynniki, które mogą kierować alokacją uwagi w naturalnych warunkach nie są jeszcze dobrze zrozumiane. W przedstawionej rozprawie prezentuję wyniki badań przeprowadzonych w celu wytyczenia zakresu selekcji uwagowej dwóch rozpoznanych źródeł istotności percepcyjnej – semantycznej spójności i znaczenia emocjonalnego.

W pierwszym badaniu sprawdzaliśmy, czy obiekty, które naruszają semantyczną strukturę scen z codziennego życia automatycznie angażują uwagę w większym stopniu, niż obiekty semantycznie spójne z kontekstem. W przeprowadzonym eksperymencie sceny zawierające obiekty były prezentowane centralnie, a peryferycznie wyświetlano niewielkie litery, które miały być rozpoznawane przez osoby badane. Prezentacja semantycznie niespójnych obiektów nie wydłużyła czasu odpowiedzi w zadaniu identyfikacji liter, co wskazuje na to, że obiekty te nie angażowały uwagi automatycznie. Jednocześnie prezentacja scen wywołujących obrzydzenie była związana z wyraźnym efektem przytrzymania uwagi. Otrzymane wyniki pokazują, że afektywnie nacechowane sceny, ale nie sceny zawierające semantyczne niespójności, mogą wywołać automatyczne zaangażowanie uwagi.

W drugim badaniu zweryfikowaliśmy, czy bodźce sygnalizujące zagrożenie mogą być wzmacniane przez mechanizmy uwagowe już na przed-świadomym etapie przetwarzania wzrokowego. Zgodnie z powszechnie przyjętym modelem, jednym z elementów reakcji obronnej wywołanej przez zagrożenie jest uwagowa selekcja zagrażającego bodźca, która zachodzi niezależnie od jego świadomego rozpoznania. W przedstawionym eksperymencie użyliśmy metody potencjałów wywołanych, żeby porównać aktywność neuronalną związaną z podprogową i nad-progową percepcją twarzy wyrażających strach i neutralny stan emocjonalny. Otrzymany wzorzec wyników sugeruje, że świadomie postrzegane twarze wyrażające strach były preferencyjnie kodowane i automatycznie przyciągały uwagę. Ponadto świadoma percepcja przestraszonych twarzy angażowała wyższe funkcje poznawcze, ale tylko gdy twarze były istotne z punktu widzenia zadania. Co ważne,

podprogowo prezentowane przestraszone twarze były preferencyjnie kodowane, ale nie znaleźliśmy dowodów na to że angażowały uwagę. Zatem nasze wyniki pokazują, że automatyczna selekcja uwagowa bodźców zagrażających jest zależna od świadomości percepcyjnej.

W trzecim badaniu ponownie przeanalizowaliśmy zebrane w badaniu drugim dane, aby sprawdzić wpływ uwagi na neuronalne korelaty świadomości wzrokowej. Zaproponowano, że wczesny potencjał wywołany nazwany Visual Awareness Negativity (VAN) stanowi specyficzny, niezależny od selekcji uwagowej neuronalny wskaźnik świadomości percepcyjnej. Zatem w przeprowadzonej analizie zbadaliśmy, czy rzeczywiście VAN nie podlega wpływowi uwagi egzogennej, związanej ze swoistą istotnością prezentowanego bodźca, oraz endogennej uwagi indukowanej wykonywanym zadaniem. Nasze wyniki pokazały, że VAN jest w dużej mierze zależny od manipulacji uwagą i to zarówno we wczesnym (140–200 ms) jak i w późnym oknie czasowym (200–350 ms). Zatem uzyskane rezultaty kwestionują pogląd jakoby VAN stanowił specyficzny, niezależny od uwagi mechanizm subiektywnego, świadomego doświadczenia.

Podsumowując, zaprezentowane badania pozwalają na lepsze zrozumienie jak selekcja uwagowa działa w naturalnych warunkach poprzez wskazanie ograniczeń przyciągania i angażowania uwagi. Nasze wyniki pokazują, że percepcja złożonych bodźców wzrokowych jakich doświadczamy w codziennym życiu polega na integracji zarówno oddolnych jak i odgórnych ścieżek przetwarzania, które wspólnie kształtują zachowanie i odpowiedź neuronalną. Uzyskane wyniki ukazują także rolę świadomości w procesie poznawczej ewaluacji bodźca oraz stanowią istotny wkład do dyskusji na temat relacji między świadomością i uwagą.

Abstract

The amount of information we encounter in our perceptual environment exceeds the capacities of our cognitive system, and thus efficient navigation in everyday situations requires a selective mechanism that prioritizes behaviorally relevant contents. This is the assumed role of the selective attention mechanism. While attention has been extensively studied in simplified, artificial settings, the factors that might drive the deployment of attentional resources in naturalistic settings are not fully understood. In the present thesis, I present the outcomes of research conducted in order to delineate the scope of attentional prioritization of two recognized sources of perceptual saliency – namely semantic congruency and affective relevance.

In the first study, we investigated whether objects that violate the semantic structure of the real-world scene automatically engage exogenous attention for longer than semantically congruent objects. The conducted experiment involved a central presentation of a scene and a peripheral presentation of a small target letter. We found that the presentation of semantically incongruent objects did not delay responses to the target identification task, which indicates that such objects did not benefit from automatic attentional engagement. At the same time presentation of disgust-evoking scenes was related to the robust attention-hold effect. The obtained results demonstrate that the affective relevance of the scene induces automatic engagement of exogenous attention, but semantic incongruency does cause a similar effect.

In the second study, we tested whether an automatic attentional response to threats can be induced at the preconscious levels of visual processing. According to the widely accepted approach, a defensive reaction to threats includes a specific attentional prioritization of the threatening stimulus that takes place regardless of conscious recognition. In the present experiment, we employed event-related potentials (ERP) to compare neural activity evoked by the subliminal and supraliminal perception of fearful and neutral facial expressions. The obtained pattern of results suggests that consciously perceived fearful faces were preferentially encoded and automatically prioritized by bottom-up attention. Furthermore, conscious perception of fearful expressions also engaged higher-order cognitive processing, but only when they were relevant to the ongoing task. Importantly, when perceived outside awareness fearful faces were still preferentially encoded, but we found no evidence for attentional prioritization. Therefore, our findings show that attentional prioritization of threats depends on perceptual consciousness.

In the third study, we reanalyzed data collected in the second study in order to investigate the influence of attention on neural correlates of visual awareness. It has been proposed that an early ERP component called Visual Awareness Negativity (VAN) constitutes a neural marker of subjective conscious experience that is independent of attentional selection. Therefore, in the conducted analysis we investigated whether VAN is indeed not affected by exogenous attention associated with the inherent saliency of presented stimuli and endogenous attention induced by task relevance. Our findings revealed that VAN was highly dependent on attentional manipulations in both early (140–200 ms) and late time windows (200–350 ms). Thus, the obtained results challenge the view that VAN constitutes a specific, attention-independent mechanism of subjective conscious experience.

Overall, the presented work contributes to a better understanding of how attention operates in naturalistic settings by elucidating the limitations of exogenous attention capture and engagement. Our findings indicate that the perception of real-world images involves the integration of bottom-up and top-down mechanisms that mutually shape the behavioral and neural response. Further, our results reveal the role of conscious evaluation and significantly add to the discussion about the relationship between awareness and attention.

1. Introduction

Our senses are continuously flooded with an overwhelming amount of sensory data. The visual environments that we encounter in our daily lives are inherently variable and cluttered with a great number of objects, characterized by different shapes, colors, and textures. Successful performance of everyday tasks such as crossing the street or finding our keys depends on the ability to select relevant information from a multitude of irrelevant sources. Nevertheless, despite the high complexity of our environment, we are able to navigate it with remarkable efficiency and relatively low effort. This ability is primarily attributed to selective attention - a cognitive mechanism that extracts and prioritizes behaviorally relevant contents and guides the allocation of perceptual resources (Carrasco, 2011; Peelen & Kastner, 2014)

The selection of relevant information from the abundance of irrelevant signals is necessary because of severe limits on the processing capacity of our perceptual and cognitive systems. The idea that stimuli presented in the visual field compete for resources can be considered one of the cornerstones of cognitive psychology and neuroscience (Broadbent, 1958; Treisman, 1960; Neisser, 1967; Kinchla, 1980). Attention directed toward stimulus biases this competition increasing the activity of neurons encoding attended information and suppressing the activity of other neurons (Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004; Beck & Kastner, 2009). Perceptual consequences of this mechanism include the enhancement of visual contrast and spatial resolution, which leads to better detection and recognition of the attended stimuli (Bashinski & Bacharach, 1980; Posner, et al., 1980; for review see: Carrasco, 2011)

Attentional selection is also essential from the neuroscience perspective, specifically for sustainable brain metabolism. The activity of neurons involved in cortical computations is related to high energy consumption, to the extent that it dominates the overall bioenergetic cost of brain activity (Attwell & Laughlin, 2001). At the same time, the amount of energy available to the brain is constant and limited (Clarke & Sokoloff, 1994), which implies that only a fraction of cortical neurons can be engaged concurrently (Barlow, 1972). These observations provide a conceptual basis for the idea that selective attention arises from the brain's metabolic constraints (Lennie, 2003).

The neural mechanisms of attentional selection span across multiple levels of visual hierarchy. The attentional modulation of visual signals begins even before perceptual information reaches the cortex, namely in the thalamus and lateral geniculate nucleus

(McAlonan et al., 2008). Further, attention directed toward visual stimulus enhances neural responses in sensory regions encoding attended location or sensory features (Hillyard et al., 1998; Luck et al., 1997; McMains et al., 2007; Carrasco, 2011). Specifically, attention modulates neural activity in the visual area 1 (V1, Luck et al., 1997; Roelfsema et al., 1998; Gandhi et al., 1999; Somers et al., 1999; McAdams & Reid, 2005; Jehee et al., 2011) and the subsequent regions of extrastriate cortex (Moran & Desimone 1985; Luck et al., 1997; Martinez et al., 2006; Natale et al., 2006; Jehee et al., 2011; Baruni et al., 2015; for review see Moore & Zirnsak, 2017). Selective enhancement of the activity of neurons encoding the attentionally relevant information is controlled by long-range feedback connections descending from higher-order cortical areas (Desimone & Duncan, 1995; Pessoa et al. 2003; Womelsdorf & Fries, 2007; Soltani & Koch, 2010; Moore & Zirnsak, 2017).

Attention is not a monolithic phenomenon. Over five decades of investigation has provided a widely accepted taxonomy of attentional processes and mechanisms, which complement each other and together contribute to the selection and maintenance of information in the cognitive system. Visual attention allocation is often accompanied by moving one's gaze toward the attended object. This mechanism constitutes overt attention and is the most common way in which attention is deployed in naturalistic settings (Henderson et al., 2003; Henderson & Pierce, 2008). However, attentional selection can also occur covertly, without actually directing one's eyes toward the stimulus (Nakayama & Mackeben, 1989). In fact, research conducted on the interaction of overt and covert attention indicates that orienting covert attention toward new locations precedes subsequent eye movements providing information on the direction in which the gaze should be directed (Van Der Lubbe et al., 2006; Kowler, 2011; Nakayama & Martini, 2011). Further, covert attention can be deployed voluntarily in order to willfully monitor information coming from a given source, or involuntarily, as an automatic response to the location of the sudden or salient stimulation. The former is known as endogenous attention and is often referred to as 'sustained' since the voluntary deployment of attentional resources takes about 300 ms and can remain at the location as long as is needed. The latter is called exogenous or 'transient' attention as the orienting response induced by external signal occurs in the first 100–120 ms after stimulus onset (Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Cheal et al, 1991; Remington et al., 1992; Hein et al., 2006; Ling & Carrasco, 2006; Liu et al., 2007). Importantly, according to the classic theory of exogenous attention orienting proposed by Posner and colleagues (1987), automatic attentional response to salient incoming stimuli includes two independent functionalities: attention shifts, defined as the movement of attention from its current location to a new one, and attention engagement, described as involvement in processing of a stimulus in the present location and a transient inability to disengage. Therefore, attention can be considered as a toolkit of related but potentially separate mechanisms, which together allow for efficient processing of information under different conditions.

1.1. Selective attention in naturalistic settings

To study the process of selecting behaviorally relevant information, experimental studies typically employ the display of simple and well-defined stimuli such as geometric shapes or patterns. Such simple stimuli have important advantages, as they can be easily defined and controlled in the laboratory setting and thus allow for a robust investigation of elementary attentional mechanisms. A classic example is the line of research on the pop-out effect, using simple stimuli characterized by one feature or a conjunction of features, and showing that stimuli that differ from the surrounding ones automatically capture attention (Lamy & Egeth, 2003; for review: Wolfe & Horowitz, 2017). However, using such simplified stimuli and conditions most likely cannot reveal the full extent of attentional mechanisms that take part in naturalistic perception. Importantly, in natural environments objects are embedded in the semantic structure of the scene and the visual appearances vary greatly across viewing conditions (Peelen & Kastner, 2014). The deployment of attention is thus highly dependent on contextual information that guides the exploration of a scene and directs perceptual resources to locations and objects expected to be most informative (Peelen & Kastner, 2014; Wu et al., 2014; Kaiser et al., 2019; Võ et al., 2019). In line with the assumption that the most informative are those stimuli that do not match other elements of the scene (the pop-out effect), it has been stated that semantically incongruent objects should benefit from attentional prioritization (Underwood et al., 2007; Wolfe & Horowitz, 2017). Importantly the automaticity and the scope of this prioritization remain a matter of vigorous debate.

Apart from the semantic relations embedded in the scenes, a widely recognized factor that may orchestrate the deployment of selective attention is emotional relevance. Automatic attentional prioritization is especially relevant when we are facing a stimulus containing information about potential danger in the environment as fast reaction in such situations can be critical for survival. Given the adaptive relevance of this mechanism, it has been proposed that our brains have evolved a highly encapsulated, subcortical system called a defensive survival circuit (LeDoux, 2012) that initiates automatic defensive reaction even before a threatening stimulus enters consciousness (LeDoux, 1998, 2012; Liddell et al., 2005; Öhman et al., 2007; Tamietto & De Gelder, 2010; Garrido et al., 2012; LeDoux & Brown, 2017). It is well documented that reaction to threats can include automatic attentional prioritization (Phelps, 2006; Carlson et al., 2009a; Troiani et al., 2014; LeDoux & Brown, 2017), but whether attentional selection of the threat-related stimuli, can be triggered outside of awareness, is a matter of ongoing debate.

1.2. *Attention and consciousness*

A phenomenon closely related to attention is perceptual consciousness, defined as the subjective experience of the sensory stimulus. Importantly, the functional role of consciousness in perception is not well defined (e.g. Rosenthal, 2008; Cohen & Dennett, 2011), with some authors assuming it has no role (Hassin, 2013). The father of American psychology, William James, stated that "focalization, concentration of consciousness are of its essence" (James, 1890). This quote illustrates a common observation that in everyday perception, our conscious subjective experience of the surrounding environment goes in lockstep with attentional focus. In extreme cases, the unavailability of attentional resources can prevent the access of otherwise highly visible stimuli into awareness, causing effects known as 'inattentional blindness' (Mack & Rock, 1998; Simons & Chabris, 1999), 'change blindness' (Simons & Levin, 1997; Simons & Rensink, 2005) or 'attentional blink' (Shapiro et al., 1997; Dux & Marois, 2009). Those observations led to the proposal that consciousness and attention are in fact identical (Posner, 1994; O'regan & Noë, 2001). This claim is still favored by some researchers (De Brigard & Prinz, 2010; Graziano, 2022), however, a growing body of empirical evidence indicates that those two phenomena can be dissociated (for review see: Maier & Tsuchiya, 2021). Specifically, it was shown that attention can operate outside of awareness modulating neural response to the stimulus even when the observer has no conscious experience of the presented content (Naccache et al. 2002; Koch & Tsuchiya, 2007; Faivre & Kouider, 2011; Hsieh et al., 2011; Kentridge, 2011). Understanding the mutual relation between attention and consciousness can provide critical insights into the function and neural mechanisms of subjective experiencing and thus in recent years it has constituted an important area of research.

2. Description of the project: the general aim

Factors orchestrating attentional selection in real-world scenarios are not fully understood. Specifying which factors can drive the deployment of attentional resources in naturalistic settings is crucial for understanding how visual perception works in everyday situations. **The aim of the presented project was to investigate how and under which circumstances two constituents of perceptual saliency – namely semantic congruency and affective relevance – capture and engage exogenous attention.**

Specifically, the first study aimed to investigate whether semantically incongruent objects automatically engage and hold exogenous attention. The experimental procedure employed the presentation of images containing a human agent interacting with an object (Mudrik et al., 2010). The object could either match the context of the interaction or not, constituting respectively semantically congruent and incongruent conditions (for instance, a person putting a chessboard in the oven). Attentional engagement in the perception of scenes was measured indirectly, by the latency of behavioral (manual) responses provided in a concurrent task, which involved the identification of simple peripherally presented stimuli. Attentional effects caused by semantically incongruent objects were compared to those accompanying perception of affective, disgust-evoking stimuli. As attentional engagement in the processing of scenes presenting disgusting content is well established, these images served as a reference in the investigation of attentional bias toward semantic incongruency.

The aim of the second study was to reveal the scope of attentional prioritization of threats. Specifically, we investigated whether threat-related stimuli can induce an automatic attentional reaction also when perceived outside the awareness. We employed the presentation of naturalistic stimuli that are known to induce robust attention-related effects, namely human faces (Kanwisher, 2000; Hedger et al., 2016). Displayed faces had either a neutral expression, or expressed fear which indicates a potential threat in the environment. Facial images were presented briefly and their conscious recognition was suppressed by a following presentation of backward masks. The presence of attentional reaction was measured with event-related potentials (ERP) extracted from the electroencephalography (EEG) signal recorded during the experimental procedure. ERPs provide robust and well-established markers of early and transient components of perceptual and cognitive processes (Luck, 2014), and thus are perfectly suited for the investigation of unconscious attentional prioritization.

Finally, the third study aimed to investigate the influence of attention on the putative neural mechanisms of perceptual consciousness. This study aimed to address one of the main challenges of consciousness research, namely identifying a set of neural events that is both sufficient and necessary for conscious experience to arise (Crick & Koch, 2003) Specific research question was motivated by a discussion regarding the potential factors confounding neural correlates of consciousness obtained by a contrastive analysis of brain activity evoked by consciously and unconsciously perceived events (Aru et al., 2012; de Graaf et al., 2012; Bola & Doradzińska, 2021). To this end, we reanalyzed neuroimaging data collected in the second study and identified patterns of electrophysiological activity associated with conscious experience of facial stimuli. Further, we investigated whether those patterns can be affected by attentional selection mechanisms, in order to define to what extent they are specifically related to perceptual consciousness. Showing that attention can influence the putative neural mechanism of consciousness has vital theoretical implications, which are discussed in concurrent sections of this thesis.

3. Description of research: background and results

3.1. Semantic congruency

Previous studies investigating attentional prioritization of semantically incongruent stimuli provided inconclusive results. For instance, research applying eye-tracking in order to capture overt attention shifts showed that incongruent objects embedded in a scene capture initial saccades, thus indicating that semantic incongruence automatically attracts attention (Loftus & Mackworth, 1978; Underwood & Foulsham, 2006; Becker et al., 2007; Underwood et al., 2007, 2008; Bonitz & Gordon, 2008). Furthermore, using a change-blindness paradigm it was demonstrated that changes applied in the semantically incongruent scenes are detected more quickly than changes applied to semantically congruent ones, which also suggests a rapid allocation of attentional resources to objects that do not match the context (Hollingworth & Henderson, 2000; LaPointe et al., 2013; Mack et al., 2017; Ortiz-Tudela et al., 2017, 2018). However, numerous other studies did not support automatic attention shifts toward semantic incongruencies (e.g. De Graef et al., 1990; Gareze & Findlay, 2007; Rayner et al., 2009; Võ & Henderson, 2009, 2011; Cornelissen & Võ, 2017). The body of evidence speaking against the automatic capture of exogenous attention by incongruent objects includes also our own experiment in which we showed, that while attention is automatically shifted toward threat-related scenes, perception of incongruent objects does not induce a similar attentional effect (Furtak et al., 2020).

While the majority of previous studies investigated whether incongruent objects *attract* attention, in the present experiment we aimed to test whether semantically incongruent objects can *hold* attention for a longer time. In favor of this hypothesis, some eye-tracking studies have demonstrated that during free exploration of the scene, participants fixate on incongruent objects more frequently and for longer than on congruent ones (Võ & Henderson, 2009, 2011). However, since in these studies, participants were allowed to explore the scene for a relatively long time, obtained results do not inform us to what extent the effect was indeed automatic and involuntary. In order to resolve whether attentional engagement in processing semantic incongruencies is in fact automatic, we employed an experimental procedure developed by Van Hoff and colleagues (2013, 2014). In their studies, authors presented participants with centrally located images and observed that the presentation of disgust-evoking contents impaired and delayed recognition of peripherally presented letters, thus indicating that disgusting stimuli hold attention. In our procedure, we used semantically congruent and incongruent scene images from the set of stimuli developed by Mudrik and colleagues (2010) and extensively used in previous studies (e.g., Mudrik et al. 2011, 2014; Moors et al., 2016; Mack et al., 2017; Biderman & Mudrik, 2018; Faivre et al. 2019; Furtak et al., 2020; Shir et al., 2021). The central presentation of an image was accompanied by the delayed onset of the peripheral target letter, and the participants' (N = 46) task was to determine as fast as possible whether a letter ‘N’ or ‘Z’ was presented (**Fig. 1**). Additionally, to congruent and incongruent scenes, we also included the disgusting images, which have been already shown to hold attention (Van Hoff et al., 2013, 2014), and happiness evoking images which served as a control condition. This was done to evaluate the sensitivity of applied methods.

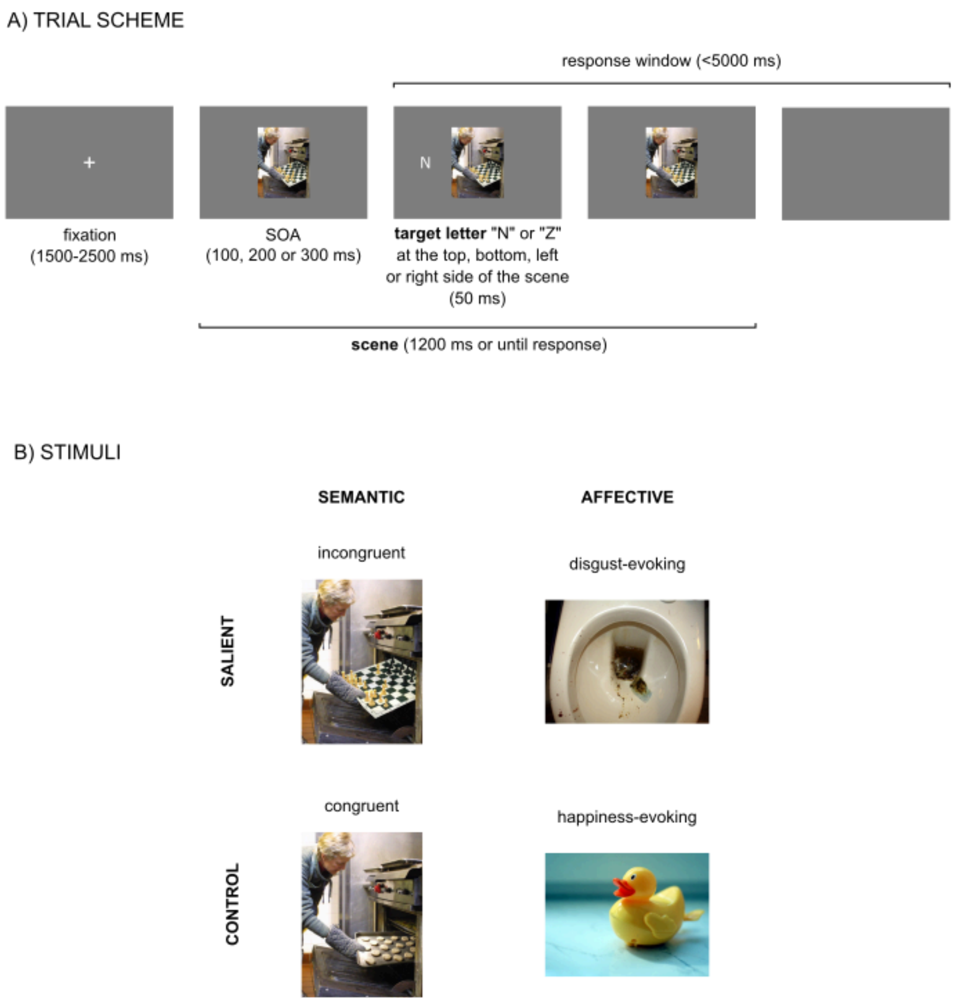

Figure 1. (A) Schematic presentation of a trial sequence and (B) representative stimuli used in the four conditions of the experiment.

The analysis of reaction times and accuracy in the letter categorization task clearly indicated that while the perception of disgust-evoking images was related to delayed and less accurate responses than the perception of happiness-evoking images, incongruent scenes did not differ from congruent ones in terms of reaction times nor accuracy (**Fig. 2**). Therefore, we concluded that disgusting scenes automatically engaged attentional resources and held them for a longer time than pleasant ones, but semantically incongruent objects did not evoke a similar attentional engagement when compared to congruent ones. Finding the attention-hold effect for disgusting images not only replicates previous findings (Van Hoff et al., 2013, 2014) but also proves that our procedure was, in principle, effective and sensitive – and thus further strengthens the interpretation of the observed null result for semantic incongruencies.

Importantly, the present study was conducted in a registered report format, which aims to improve the robustness and replicability of empirical studies (Chambers & Tzavella, 2022). This means that the introduction, hypotheses, methods, and analysis plan were peer-reviewed before the study commenced, and could not have been altered afterward. Such a procedure prevents post-hoc interpretations, counteracts publication bias, and overall enhances the quality of published research.

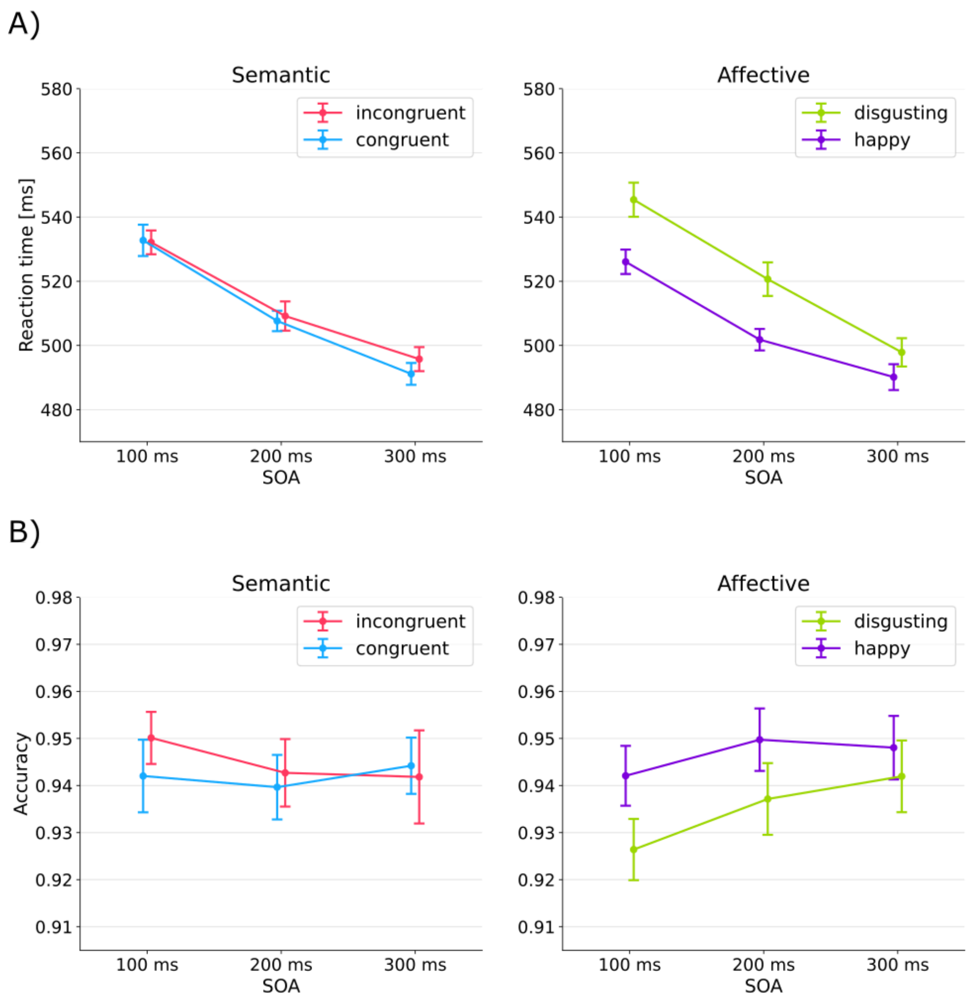

Figure 2. (A) Reaction times and (B) response accuracy scores obtained for semantic (left plot) and affective (right plot) sets of stimuli. Dots represent means, while whiskers designate 95% confidence intervals calculated using the Cousineau–Morey method for within-subjects designs (Morey, 2008).

3.2. *Affective relevance*

Signals of threats induce a robust and automatic defense response associated with the activation of the amygdala, even when perceived unconsciously (Whalen et al., 1998; Morris et al., 1999; Williams et al., 2004a, 2004b, 2006; Liddell et al., 2005; Pegna et al., 2005; Diano et al., 2017). It has been shown that subliminal perception of fear-evoking images leads to autonomic nervous system responses (Esteves et al., 1994; Gläscher & Adolphs 2003; Ruiz-Padial et al., 2005; Tamietto et al., 2009, 2015), hormone secretion (van Honk et al., 1998, 2000), and preparation of reflexive behavioral reactions such as avoidance or freezing (Hamm et al., 2003; Stewart et al., 2012). Initial evidence indicated that preconscious reaction to threats includes also automatic attention capture (see Tamietto & DeGelder, 2010). For instance, multiple studies have found that threatening images gain preferential access to awareness when they have to compete for attentional resources with a concurrent demanding task (inattentional blindness paradigm, Milders et al., 2006; Maratos et al., 2008; Rosa et al., 2014) or with other non-threatening stimuli (binocular rivalry, continuous flash suppression, Yang et al., 2007; Bannerman et al., 2008; Ritchie et al., 2011; Gerdes & Alpers, 2014). Further, it was shown, that unconsciously perceived threats modulated reaction times (RTs) to the subsequent target stimuli, which indicates that they can capture and engage spatial attention (Mogg & Bradley, 1999; Fox, 2002; Carlson & Reinke, 2008; Carlson et al., 2009b, 2016; Carlson & Mujica-Parodi, 2015).

Importantly, despite a wide body of evidence speaking in favor of unconscious attentional prioritization of threats, a recent meta-analysis conducted by Hedger and colleagues (2016) found that pooled attentional effects observed in previous studies are small or even inconsistent. Further, they found that the majority of analyzed studies collected insufficient sample sizes, and thus concluded the effects reported as statistically significant might in fact have been incidental. Moreover, Hedger and colleagues (2016) pointed out that many previous studies investigating attentional reaction to unconsciously perceived signals of threat did not test whether the employed method of awareness suppression was successful, and thus the observed attentional bias might have been caused by residual awareness of presented stimuli (see also: Pessoa et al., 2005; Szczepanowski & Pessoa, 2007; Lähteenmäki et al., 2015; Mudrik & Deouell, 2022). Indeed, a few studies that applied more restrictive masking procedures did not find evidence for attentional prioritization of threats (Koster et al., 2007; Hedger et al. 2015, 2019). Finally, while some previous studies reported that subliminally presented threatening stimuli can enhance neural activity evoking ERP patterns typically associated with attentional selection (Liddell et al., 2004; Williams et al., 2004c; Kiss & Eimer, 2008; Balconi & Mazza, 2009; Jiang et al., 2009; Pegna et al., 2011; Qiu et al., 2023) other suggested the opposite effect (Wang et al., 2016; Jiang et al., 2018).

In the face of those conflicting results the present study aimed to provide robust evidence either in favor or against the unconscious attentional prioritization of threat-related stimuli. Considering the outcomes of the meta-analysis conducted by Hedger and colleagues (2016) we have collected a sample of participants sufficient to attain a statistical power of 95% (N = 46) and thoroughly controlled the visibility of presented stimuli. Further, in order to maximize the chances of obtaining significant results we employed a presentation of fearful face images that were shown to cause more robust attention-related effects than any other threat-related stimulus (Hedger et al., 2016). Faces were displayed bilaterally for 16 ms and followed either by an empty screen (supraliminal, conscious condition) or backward masks, which interfered with visual processing resulting in subliminal perception (unconscious condition, **Fig. 3**). Participants performed two tasks: in one of them faces were task-relevant targets (identification task), in the other one they were presented as task-irrelevant distractors (dot-probe task). We recorded brain activity using EEG and investigated the ERP response to the presentation of fearful and neutral facial expressions presented either as task-relevant targets or as task-irrelevant distractors, perceived either consciously or subliminally. In the analysis, we searched for the patterns of neural activity indicating that subliminal perception of fearful faces caused attentional capture or engagement.

Because the experimental procedure involved an identification task in which participants had to indicate the expression of one of the presented faces, this allowed us to measure their ability to categorize facial stimuli in a condition in which the presentation of faces was followed by the masks (unconscious condition) and in a condition in which masks were not presented (conscious condition). Analysis of behavioral responses indicated that in the conscious condition participants, performance in discriminating emotional expressions was close to the chance level, while in the conscious condition, it was considerably higher (**Fig. 3**). This indicates that the presentation of masks interrupted conscious recognition of the emotional value of the stimulus, while when stimuli were unmasked, participants were able to consciously detect presented contents.

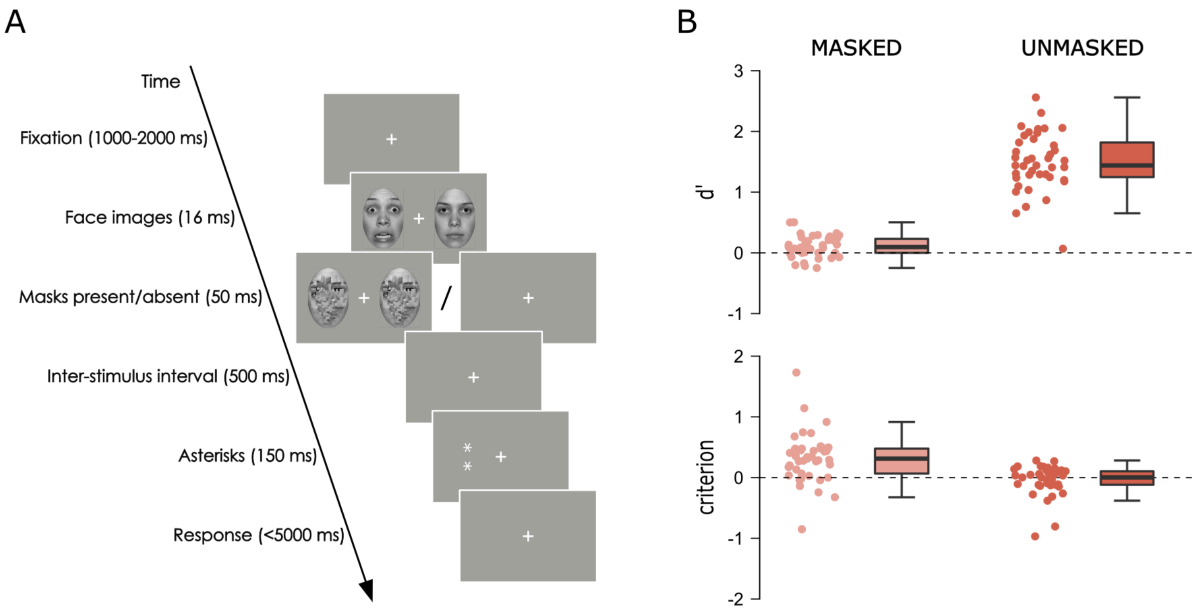

Figure 3. (A) Schematic presentation of an experimental trial. (B) D' and criterion values obtained in the masked and unmasked ID tasks. For each condition and SDT measure, the dots present the raw data points i. e. participants. The box depicts descriptive statistics; the horizontal lines inside boxes indicate the median values across participants; the box boundaries indicate the lower to upper quartile values; the whiskers indicate the first value exceeding 1.5 of QD below or above the lower or the upper quartile.

Analysis of the ERP signal included the investigation of several components (for review see: Luck, 2012; **Fig. 4 and 5**). First, we measured amplitudes of the P1 component which reflects the processing of the low-level perceptual features (Di Russo et al., 2002; Jeffreys & Axford, 1972), and revealed that it was not influenced by the emotional expressions of the presented facial stimuli neither during conscious nor unconscious presentations. Second, we tested the N170 component, which is considered to reflect face encoding (Bentin et al., 1996; Eimer, 2000; Blau et al., 2007; Hinojosa et al., 2015), and showed that it responded preferentially to fearful faces regardless of the stimulus visibility and task-relevance, however, in the unconscious condition this effect was present only at the trend level ($p < 0.1$). Third, we analyzed mid-latency components, which are considered markers of bottom-up attentional prioritization (Carretié et al., 2004, Schupp et al., 2004), and obtained evidence that the amplitude of the EPN component was enhanced by fearful expressions; but this effect was only present in the conscious condition, and not in the unconscious condition. A similar pattern of results was obtained for the lateralized N2pc component, which indicates shifts of spatial attention focus (Luck & Hillyard, 1994; Woodman & Luck, 2003; but see Zivony et al., 2017). Specifically, the N2pc amplitude was enhanced in response to fearful face presentation, but only when stimuli were consciously perceived. Finally, the amplitude of the P3 component lateralized SPCN (sustained posterior contralateral negativity), both of which have been associated with the sustained engagement of cognitive resources (Polich, 2007, 2012; Jolicœur et al., 2008; Sessa et al., 2011), was enhanced only during conscious perception of fearful faces, and only when facial stimuli were relevant to the ongoing task.

Overall, while we observed a robust attentional response to fearful faces presented in the conscious (unmasked) condition, unconscious perception of fearful expressions was not associated with any attentional effects. Specifically, even though unconsciously perceived fearful faces evoked enhanced response of the N170 component, indicating structural encoding of facial stimuli, we did not observe any unconscious threat-related effects on the subsequent components that index bottom-up attentional selection (P2, N2, EPN components), spatial attention orienting (N2pc component), or engagement of attentional resources (SPCN, P3 components). In light of those results, we concluded that the attentional prioritization of threat-related stimuli does not emerge at the preconscious stage of stimulus evaluation, which contradicts a widely accepted model of fear reaction (LeDoux & Brown, 2017)

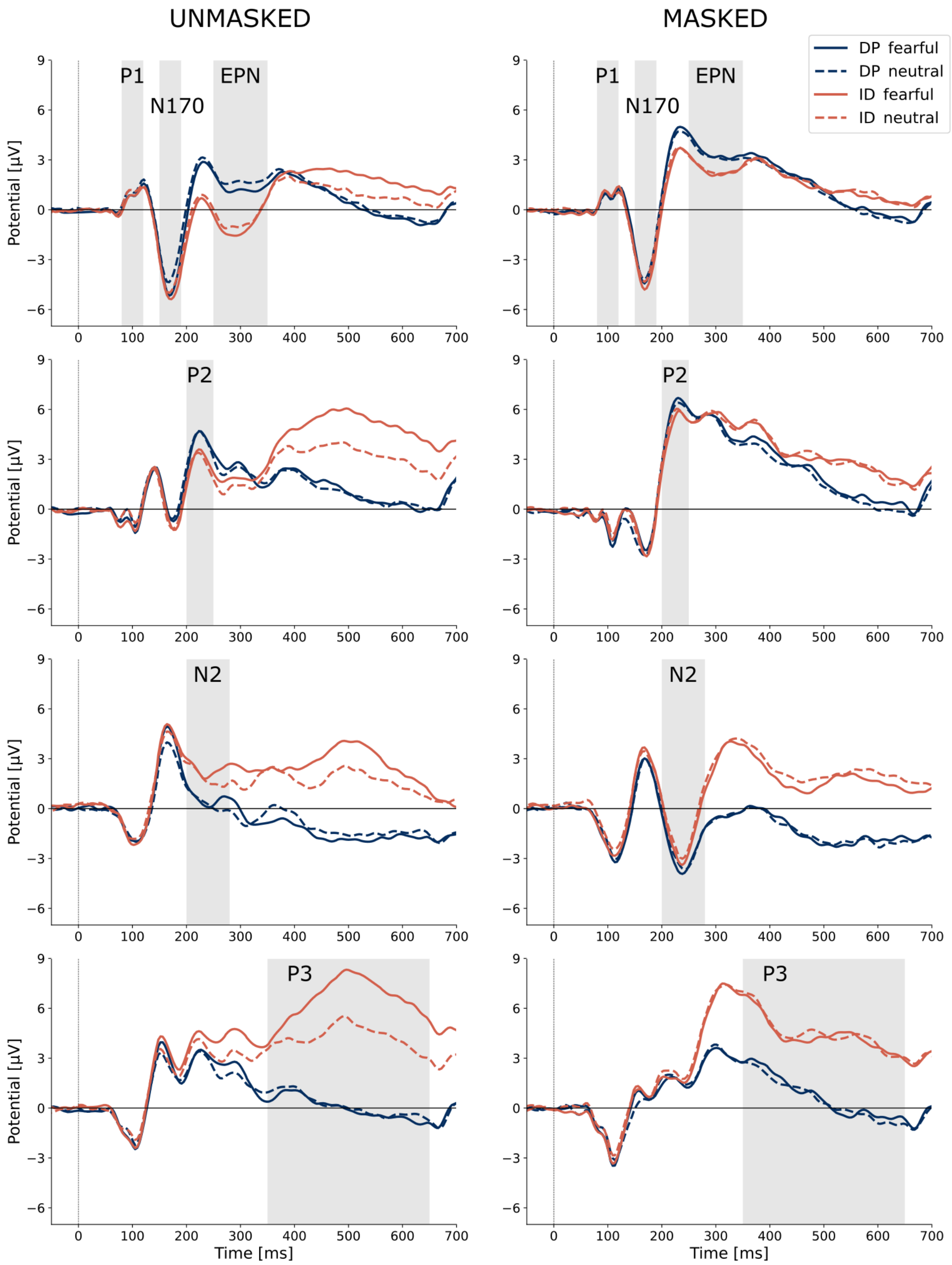

Figure 4. ERPs time-locked to the onset of face images, calculated for trials containing two fearful or two neutral faces. Within each panel, ERPs divided with respect to the task (DP – Dot-probe; ID – Identification) and facial expression (neutral or fearful) are plotted. The left column presents ERPs obtained in the unmasked condition; the right column presents data from the masked condition. In the first row, ERPs were averaged over the P7, P8, PO7, PO8, P9, P10 electrodes; in the second row, the ERPs were calculated from averaged PO3, POz, PO4, O1, Oz, O2; in the third row, they are averaged from F1, F2, Fz, FC1, FC2, FCz; and in the fourth row, they are averaged from the CP1, CPz, CP2, P1, Pz, P2 electrodes. The time windows used for statistical analysis of particular components are highlighted in gray. Due to the design of the statistical analysis, significant effects are not depicted in the figure.

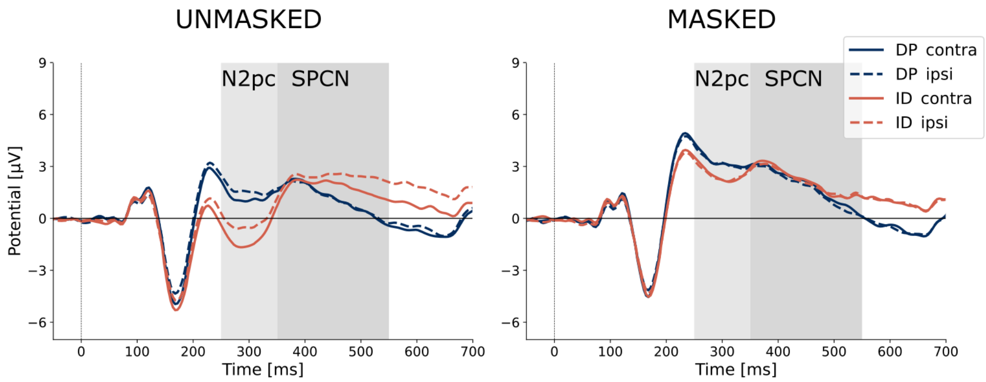

Figure 5. Lateralized ERPs time-locked to the onset of face images, calculated for trials containing one fearful and one neutral face. The left column presents ERPs obtained in the unmasked condition; the right column presents data from the masked condition. ERPs were calculated from the P7, PO7, and P9 electrodes on the left side and from the P8, PO8, and P10 electrodes on the right side. The time windows used for statistical analysis of particular components are highlighted in gray.

3.3. *Attentional modulation of neural correlates of consciousness*

Identifying neural correlates of consciousness (NCC), defined as neural processes that are both necessary and sufficient for a given conscious experience to occur, constitutes one of the main aims of consciousness research (Crick & Koch, 2003). Recently it was proposed that the most plausible neural correlate of perceptual awareness is the recurrent activity of modality-specific sensory cortices occurring shortly after stimulus onset (review: Förster et al., 2020; Dembski et al., 2021). This claim is supported by electrophysiological studies, which showed that consciously perceived stimuli – when compared to undetected or unconscious ones – evoke a negative deflection of the early components of ERP waveform (150-350 ms) recorded over sensory regions. In the visual domain, this negative deflection is termed Visual Awareness Negativity (VAN; Koivisto & Revonsuo, 2010) and can be observed on occipitotemporal EEG electrodes. What favors VAN as a correlate of visual awareness is that it can be observed irrespective of the task performed by a participant (Pitts et al., 2014; Shafto & Pitts, 2015; Koivisto & Grassini, 2016; Eklund & Wiens, 2018) and its amplitude positively correlates with visibility ratings (Andersen et al., 2016; Koivisto & Grassini, 2016; Derda et al., 2019).

Importantly, neural reaction to external stimulus relies on the multitude of complex and simultaneous processes related to the perceptual and cognitive evaluation of incoming sensory signals. Therefore, establishing that a given process is a proper NCC requires demonstrating that it is not reflecting other, co-occurring mechanisms that are not related to consciousness per se (Aru et al., 2012; de Graaf et al., 2012). Importantly, selective attention is one of the processes that can induce ERP effects which are very similar to VAN in terms of timing and topography, such as EPN or N2pc components (review: Luck, 2012; Luck & Kappenman, 2013). Therefore, selective attention might constitute an important confound in studies aiming to identify early correlates of consciousness (Bola & Doradzińska, 2021).

Previous work aiming to dissociate the early ERP correlates of awareness and selective attention provided inconclusive results, with some studies indicating that VAN is not modulated by attention-related factors, and thus it should be considered a specific index of phenomenal awareness (Koivisto & Revonsuo, 2007; Koivisto et al., 2008; Dellert, et al 2022); and others challenging this conclusion by showing that selective attentional can influence the amplitude of VAN (Koivisto et al., 2005, 2006, 2009; Koivisto & Revonsuo, 2008; Pitts et al., 2014; Zotto & Pegna, 2015; Andersen et al., 2022). Therefore, in the present study, we decided to reanalyze data collected in the second experiment presented in this thesis. Importantly, as neural underpinnings of consciousness constitute a different research topic than the correlates of unconscious fear processing investigated in the original study, the present analysis constituted a separate study. In the reanalysis, we identified VAN evoked by the presentation of facial stimuli and systematically examined the impact of attentional manipulations included in the experimental procedure. Specifically, we tested to what extent VAN is influenced by exogenous attention capture and engagement related to the affective relevance of presented stimuli, and by the impact of endogenous attention related to task relevance of presented stimuli. As it was suggested that VAN comprises two subcomponents, which might exhibit different relations with selective attention, namely the early one overlapping with the N1 component, and a late one that overlaps with the P2 and N2 components (Koivisto et al., 2005, 2009; Koivisto & Revonsuo, 2007, 2008; Railo et al., 2011) we analyzed the early and the late part of VAN separately.

Our results indicate that early VAN is gated by attentional engagement and thus can be completely suppressed when stimuli are non-salient or task-irrelevant (**Fig. 6**). Additionally, we found that when faces were perceived consciously both endogenous and exogenous attention produced a negative deflection of the ERP waveform that was similar to VAN. In the late time window, VAN was observed regardless of the experimental condition, but it was robustly modulated by both endogenous and exogenous attention. Furthermore, in the conscious condition both, stimulus saliency and task relevance, produced a VAN-like negative deflection of the ERP waveform. Importantly, the negative deflection of the ERP signal evoked by endogenous attention was also present in the unconscious condition. Therefore, we concluded that since the amplitude of both the early (140–200 ms) and late (200–350 ms) VAN is significantly modulated by both exogenous and endogenous attention then VAN should not be considered a specific marker of consciousness. We rather argue that VAN, at least to a certain extent, reflects attentional prioritization of presented stimulus.

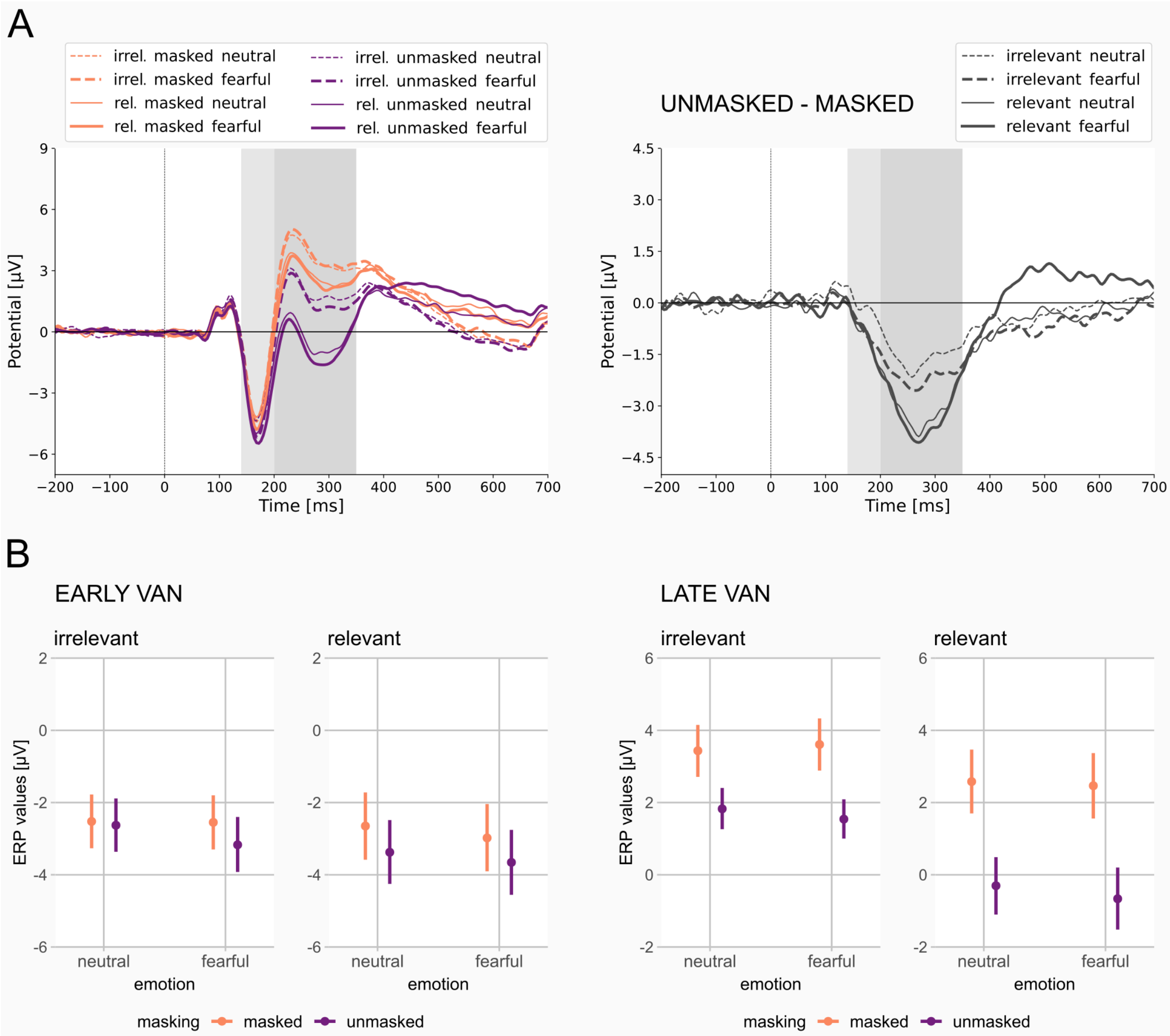

Figure 6. ERP values recorded in the posterior-temporal cluster of electrodes (P7, PO7, P9, P8, PO8, and P10) in response to trials with two fearful or two neutral faces. (A) ERPs time-locked to the onset of face images. In the left panel, ERPs obtained in the masked and unmasked conditions are plotted separately; the right panel depicts the differential waveforms which resulted from the subtraction of the potentials registered in the masked condition from those registered in the unmasked condition. The time windows used for statistical analysis of early and late VAN are highlighted in light and dark gray, respectively. (B) The estimated ERP signal values in the early (left panel) and late (right panel) VAN time windows with respect to task relevance, masking condition, and emotional expression of presented faces. Dots depict estimated values; error bars depict 95% credibility intervals derived from the statistical model.

4. Discussion

Mechanisms of selective attention are usually investigated with arrays of mutually independent stimuli defined by simple physical features. While studies employing those simple setups provided crucial insights into the mechanisms of attentional selection, it is not well understood how their findings might translate into more naturalistic settings. Scenes we encounter in our daily lives are inherently more complex and crowded with objects. What allows us to effectively navigate cluttered displays is the semantic structure of the environment that introduces expectations about the locations and identities of objects (Bar, 2004; Peelen & Kastner, 2014). Further, natural scenes often contain socially relevant cues such as other people's faces, which are particularly informative as they signal forthcoming interactions and their potential outcomes. For instance, emotional facial expressions can also carry information about potential dangers in the environment, and fast recognition and reaction to such threats can be critical for survival. Thus, it has been proposed that threatening stimuli are processed within a separate, dedicated neural circuit (LeDoux & Brown, 2017). Studies presented in this thesis investigated mechanisms of selective attention accompanying the perception of naturalistic stimuli. Specifically, we aimed to reveal the scope and the automaticity of attentional reaction to objects that violate the semantic structure of real-world scenes, and to images of fearful faces, which are natural indicators of threats.

Expectations arising from semantic regularities present in naturalistic displays effectively facilitate object recognition (Peelen & Kastner, 2014; Wu et al., 2014; Kaiser et al., 2019; Wolfe & Horowitz, 2017; Võ et al., 2019). At the same time, objects that violate those expectations are most informative, as they convey information that cannot be derived from their surroundings. Therefore it has been stated that semantic incongruencies should benefit from attentional prioritization (Underwood et al., 2007; Wolfe & Horowitz, 2017). While most previous studies, including previous work conducted by our team (Furtak et al., 2020), investigated the attraction of attention by semantically incongruent objects; in the work presented in this thesis we focused on the mechanism of attentional engagement. Importantly, collected data indicate that incongruent objects do not engage and hold attention for a longer time than congruent ones. More generally, our findings suggest that, unlike simple physical features, semantic regularities embedded in natural scenes do guide attention automatically (review: Wolfe & Horowitz, 2017). However, the presented work investigated only a very specific case of semantic incongruence, and certainly, more studies are needed to comprehensively establish the role of semantic dependencies in attentional selection

It has been shown that the recognition of incongruent objects requires greater involvement of cognitive resources as they do not benefit from contextual facilitation (Bar, 2004), and thus it was suggested that such stimuli should preferentially engage selective attention. In line, several eye-tracking studies have found that during free exploration of a scene, semantically incongruent objects hold participants' gaze for a longer time than congruent ones (Henderson et al., 1999; Underwood et al., 2008; Võ & Henderson, 2009, 2011; Cornelissen & Võ, 2017). Importantly, eye-tracking studies measure overt attention, which can operate independently from covert attention orienting. Further, the experimental procedures used in those studies were not designed to capture the automatic engagement of exogenous attention, as presented objects were relevant to the task (indicating the engagement of endogenous attention, as discussed by Cornelissen & Võ, 2017) and participants were encouraged to explore presented scenes at their own pace. Therefore the discrepancies between previous findings and data obtained in our study can be attributed to the fact that they measured different attentional mechanisms. While semantic structure violations might engage overt or endogenous attention, according to our results, they neither capture (Furtak et al., 2020) nor hold exogenous attention in an automatic manner.

Importantly, our experiment also included a “positive control” condition which involved the presentation of disgust-evoking and happiness-evoking scenes. We found robust evidence that attention is preferentially and automatically engaged in the processing of disgusting images. This result not only strengthens the interpretation of the null effect observed for semantically incongruent objects by showing that our procedure was in principle sensitive enough to capture the attention-hold effect but also provides a replication and extension of studies conducted by Van Hooff and colleagues (2013, 2014). The main limitation of their work was the narrow set of emotional images employed in the procedure (only 10 images per emotional category from the IAPS set; Lang et al., 2008). In contrast, our study employed a significantly larger set of images (50 per emotional condition) selected from the NAPS set, which provides a bigger pool of modern and culturally neutral emotional images (Marchewka et al., 2014; Riegel et al., 2016). Thus, our study not only replicated Van Hooff and colleagues’ findings (2013, 2014) but also confirmed the robustness and generalizability of automatic attention engagement in the processing of disgust-evoking scenes.

Rapid attentional selection of negatively charged stimuli was further confirmed by the outcomes of the second study presented in this thesis, employing conscious and unconscious presentations of fearful facial expressions. The pattern of ERP activations observed in the conscious condition indicated that the perception of fearful faces results in greater involvement of both automatic (i.e. task-independent) and strategic (i.e. task-dependent) attentional resources, in comparison to the perception of neutral expressions. Those findings are consistent with the existing literature and indicate that threat-related stimuli automatically capture and engage exogenous attention (e.g. Schupp et al., 2004; Eimer & Kiss, 2007; Sessa et al., 2011; for a review see: Olofsson et al., 2008; Hajcak et al., 2010; MacNamara et al., 2013; Gupta et al., 2019; Schindler & Bublatzky, 2020). As the involvement of strategic attentional resources indicated by late ERP components was observed only in the task-relevant conditions, our findings support the view that top-down, context-related factors can to some extent shape the scope of attentional prioritization of threats (Pessoa et al., 2002, 2005; Holmes et al., 2003; Silvert et al., 2007; Eimer & Kiss, 2008; Brosch & Wieser, 2011; Dou et al., 2021; Tipura & Pegna, 2022).

Importantly, it has been proposed that automatic attentional prioritization of threats can occur already in the preconscious stages of processing. Specifically, according to the 'low-road' hypothesis, perception of threats activates subcortical areas of the defensive circuit, which are functionally coupled to attention-related cortical regions, which in turn induce automatic and unconscious attentional selection of threat-related stimulus (Phelps, 2006; Carlson et al., 2009a; Troiani et al. 2014; LeDoux & Brown, 2017). However, our results obtained in the unconscious condition contradict this proposal, showing that subliminally perceived fearful faces did not differ from neutral ones in terms of evoked neural activity, therefore indicating no preconscious attentional bias toward signals of threat. Our findings are in line with several behavioral (Koster et al., 2007; Hedger et al., 2015, 2019) and electrophysiological studies (Pegna et al., 2008; Zotto & Pegna, 2015; Grassini et al., 2016; Schlossmacher et al., 2017; Qiu et al., 2022a), which also found that threat signals did not benefit from preconscious attentional prioritization. Overall, these results support the 'many roads' hypothesis, which assumes that reaction to threats involves a complex interplay between subcortical and cortical areas, is based on a conscious evaluation of incoming perceptual signals, and involves top-down endogenous attention (Pessoa & Adolphs, 2010).

Lack of attentional prioritization of subliminally presented fearful faces is particularly striking as the perception of faces, in general, is considered highly automatic (Kanwisher, 2000; Kanwisher & Yovel, 2006; Crouzet et al., 2010; Richler et al., 2011) and to some extent preconscious (review: Axelrod et al., 2015; Mudrik & Deouell, 2022). Previous studies have shown that relevant facial features, such as eye gaze direction (Yokoyama et al., 2013) or self-relevance (Wójcik et al., 2019; Bola et al., 2021), can indeed unconsciously bias attention. Therefore, by elucidating the limitations of unconscious attentional selection our findings constitute a relevant input to the ongoing discussion regarding the capabilities of unconscious processing (Hassin, 2013; Hesselmann & Moors, 2015; Goldstein & Hassin, 2017; Melnikoff & Bargh, 2018; Hirschhorn et al., 2021).

Finally, data collected in the second study allowed for the investigation of putative neural mechanisms of consciousness, and their relation to exogenous and endogenous attention. Specifically, in the third article presented in this thesis, we analyzed early ERP signatures of perceptual awareness, namely VAN (Förster et al., 2020; Dembski et al., 2021), and assessed how they were influenced by the emotional expressions (exogenous attention) and task relevance (endogenous attention) of presented facial stimuli. Our findings indicate that attentional selection enhanced the magnitude of VAN, with endogenous attention operating both early and late time windows of this component, and exogenous attention impacting VAN primarily in the late time window. Further, we observed a complete suppression of early VAN induced by the manipulation of endogenous attention, which indicates that this subcomponent is not necessary for awareness. Finally, we found an unconscious VAN-like activity evoked by attentional manipulations in both early and late time windows suggesting that this component is also not sufficient for conscious experience to occur. Those findings have several theoretical implications that are of relevance to the ongoing debate regarding neural underpinnings of conscious perception (see: Boly et al., 2017).

VAN is assumed to reflect the activity of local feedback projections in the modality-specific sensory cortex, therefore it is considered to provide support for the Recurrent Processing Theory (RPT), which proposes that recurrent processing in sensory regions is a specific neural mechanism of phenomenal experience (Lamme, 2000, 2003, 2006; Lamme & Roelfsema, 2000). Importantly, RPT assumes that phenomenal experience is completely independent of cognitive mechanisms such as attentional selection (Lamme, 2004). While several previous studies have shown that ERP effects related to selective attention might overlap with the late part of VAN (i.e., after 200 ms; Koivisto et al., 2005, 2009; Koivisto & Revonsuo, 2008; Zotto & Pegna, 2015; Qiu et al., 2022a, 2022b), it was specifically stated that its early part should remain free from the influence of attentional processes (Railo et al., 2011). Our findings challenge this view by demonstrating that the modulation of VAN attention-related factors begins already in the early time window. Our results contradict RPT and suggest that in order to hold their assumptions about the independence between awareness and attention, this theory should develop a different proposition for the neural mechanism of consciousness.

Employing presentations of complex naturalistic stimuli in experimental procedures is not trivial, as complex, real-world images had to be controlled in terms of low-level physical features, semantic associations they induce, and many other aspects that do not apply when using simple visual shapes or geometric patterns. Therefore, in the presented work I have made every effort to select appropriate sets of stimuli and match them in terms of visual features. I have adopted images from well-established sets of visual stimuli that have been also extensively used in previous studies (i.e. Tottenham et al., 2009; Mudrik et al, 2010; Marchewka et al., 2014; Riegel et al., 2016) and thoroughly discussed all the potential confounds introduced by differences between conditions. Furthermore, all conducted analyses comprised advanced statistical methods including Bayesian hypothesis testing and hierarchical models. Such an approach enhances the statistical power of investigated effects and strengthens our conclusions regarding null results. Finally, all data and materials included in this thesis have been published in freely available repositories (i.e. OSF, Github, PsyArchiv), therefore complying with open science practices.

5. Summary and conclusions

Studies using complex, ecological stimuli are crucial to fully understand how our attention operates in everyday scenarios. Experimental findings presented in this thesis indicate that attentional mechanisms that may have been synthesized in studies employing simple, artificial settings, do not translate easily into naturalistic perception. Specifically, while our previous study indicated that violation of the semantic structure of the scene does not capture exogenous attention (Furtak et al., 2020), the findings presented in this thesis demonstrate that it does not benefit from the automatic engagement of covert attention. Further, perception of threat-related signals induces a robust attentional reaction, but only when accompanied by a conscious experience. Finally, the correlates of perceptual awareness can be modulated by attentional selection of presented content. Discovered limitations of exogenous attention capture and engagement indicate that real-world perception relies on complex interrelations between top-down and bottom-up processes that mutually shape the behavioral and neural response. Finally, our results highlight the importance of conscious evaluation and reveal the interdependency between awareness and attention.

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