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

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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. 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 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.

References

- 1. Andersen, L. M., Pedersen, M. N., Sandberg, K., & Overgaard, M. (2016). Occipital MEG activity in the early time range (< 300 ms) predicts graded changes in perceptual consciousness. *Cerebral cortex*, *26*(6), 2677–2688.
- Andersen, L. M., Vinding, M. C., Sandberg, K., & Overgaard, M. (2022). Task requirements affect the neural correlates of consciousness. *European Journal of Neuroscience*, 56(10), 5810–5822.
- 3. Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*(2), 737–746.
- 4. Attwell, D., & Laughlin, S. B. (2001). An energy budget for signaling in the grey matter of the brain. *Journal of Cerebral Blood Flow & Metabolism*, *21*(10), 1133–1145.
- 5. Axelrod, V., Bar, M., & Rees, G. (2015). Exploring the unconscious using faces. *Trends in cognitive sciences*, *19*(1), 35–45.
- 6. Balconi, M., & Mazza, G. (2009). Consciousness and emotion: ERP modulation and attentive vs. pre-attentive elaboration of emotional facial expressions by backward masking. *Motivation and Emotion*, *33*, 113–124.
- Bannerman, R. L., Milders, M., De Gelder, B., & Sahraie, A. (2008). Influence of emotional facial expressions on binocular rivalry. *Ophthalmic and Physiological Optics*, 28(4), 317–326.
- 8. Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, 5(8), 617-629.
- 9. Barlow, H. B. (1972). Single units and sensation: a neuron doctrine for perceptual psychology?. *Perception*, *1*(4), 371–394.
- Baruni, J. K., Lau, B., & Salzman, C. D. (2015). Reward expectation differentially modulates attentional behavior and activity in visual area V4. *Nature Neuroscience*, 18(11), 1656-1663.
- Bashinski, H. S., & Bacharach, V. R. (1980). Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Perception & psychophysics*, 28, 241–248.
- 12. Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, *49*(10), 1154–1165.
- 13. Becker, M. W., Pashler, H., & Lubin, J. (2007). Object-intrinsic oddities draw early saccades. *Journal of Experimental Psychology: Human Perception and Performance*, 33(1), 20.

- 14. Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of cognitive neuroscience*, 8(6), 551–565.
- Biderman, N., & Mudrik, L. (2018). Evidence for implicit—but not unconscious—processing of object-scene relations. *Psychological science*, 29(2), 266–277.
- Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behavioral and brain functions*, *3*, 1–13.
- 17. Bola, M., & Doradzińska, Ł. (2021). Perceptual awareness negativity—does it reflect awareness or attention?. *Frontiers in Human Neuroscience*, 15, 742513.
- 18. Bola, M., Paź, M., Doradzińska, Ł., & Nowicka, A. (2021). The self-face captures attention without consciousness: Evidence from the N2pc ERP component analysis. *Psychophysiology*, *58*(4), e13759.
- Boly, M., Massimini, M., Tsuchiya, N., Postle, B. R., Koch, C., & Tononi, G. (2017). Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? Clinical and neuroimaging evidence. *Journal of Neuroscience*, 37(40), 9603–9613.
- 20. Bonitz, V. S., & Gordon, R. D. (2008). Attention to smoking-related and incongruous objects during scene viewing. *Acta Psychologica*, *129*(2), 255–263.
- 21. Broadbent, D.E. (1958). Perception and communication Pergamon Press
- 22. Brosch, T., & Wieser, M. J. (2011). The (non) automaticity of amygdala responses to threat: on the issue of fast signals and slow measures. *Journal of Neuroscience*, *31*(41), 14451–14452.
- 23. Carlson, J. M., & Reinke, K. S. (2008). Masked fearful faces modulate the orienting of covert spatial attention. *Emotion*, 8(4), 522.
- 24. Carlson, J. M., Reinke, K. S., & Habib, R. (2009a). A left amygdala mediated network for rapid orienting to masked fearful faces. *Neuropsychologia*, 47(5), 1386–1389.
- 25. Carlson, J. M., Fee, A. L., & Reinke, K. S. (2009b). Backward masked snakes and guns modulate spatial attention. *Evolutionary Psychology*, 7(4), 147470490900700404.
- Carlson, J. M., & Mujica-Parodi, L. R. (2015). Facilitated attentional orienting and delayed disengagement to conscious and nonconscious fearful faces. *Journal of Nonverbal Behavior*, 39, 69–77.

- 27. Carlson, J. M., Torrence, R. D., & Vander Hyde, M. R. (2016). Beware the eyes behind the mask: The capture and hold of selective attention by backward masked fearful eyes. *Motivation and Emotion*, *40*, 498–505.
- 28. Carrasco, M. (2011). Visual attention: The past 25 years. Vision Research, 51(13), 1484–1525
- 29. Carretié, L., Hinojosa, J. A., Martín-Loeches, M., Mercado, F., & Tapia, M. (2004). Automatic attention to emotional stimuli: neural correlates. *Human brain mapping*, 22(4), 290–299.
- 30. Chambers, C. D., & Tzavella, L. (2022). The past, present and future of Registered Reports. *Nature human behaviour*, 6(1), 29–42.
- Cheal, M., Lyon, D. R., & Hubbard, D. C. (1991). Does attention have different effects on line orientation and line arrangement discrimination?. *The Quarterly Journal of Experimental Psychology*, 43(4), 825–857.
- 32. Clarke, D.D., & Sokoloff L. (1994) Circulation and energy metabolism of the brain. In *Basic Neurochemistry* (pp. 645-660). Raven.
- 33. Cohen, M. A., & Dennett, D. C. (2011). Consciousness cannot be separated from function. *Trends in cognitive sciences*, *15*(8), 358–364.
- Cornelissen, T. H., & Võ M. L. H. (2017). Stuck on semantics: Processing of irrelevant object-scene inconsistencies modulates ongoing gaze behavior. *Attention, Perception, & Psychophysics, 79*(1), 154–168.
- 35. Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6(2), 119-126.
- 36. Crouzet, S. M., Kirchner, H., & Thorpe, S. J. (2010). Fast saccades toward faces: face detection in just 100 ms. *Journal of Vision*, *10*(4), 16–16.
- 37. De Brigard, F., & Prinz, J. (2010). Attention and consciousness. *Wiley interdisciplinary reviews: Cognitive science*, *1*(1), 51–59.
- 38. De Graaf, T. A., Hsieh, P. J., & Sack, A. T. (2012). The 'correlates' in neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*(1), 191–197.
- 39. De Graef, P., Christiaens, D., & d'Ydewalle, G. (1990). Perceptual effects of scene context on object identification. *Psychological Research*, *52*(4), 317–329.
- 40. Dellert, T., Krebs, S., Bruchmann, M., Schindler, S., Peters, A., & Straube, T. (2022). Neural correlates of consciousness in an attentional blink paradigm with uncertain target relevance. *NeuroImage*, 264C, 119679.
- 41. Dembski, C., Koch, C., & Pitts, M. (2021). Perceptual awareness negativity: a physiological correlate of sensory consciousness. *Trends in Cognitive Sciences*, 25(8), 660–670.
- Derda, M., Koculak, M., Windey, B., Gociewicz, K., Wierzchoń, M., Cleeremans, A., & Binder, M. (2019). The role of levels of processing in disentangling the ERP signatures of conscious visual processing. *Consciousness and Cognition*, 73, 102767.
- 43. Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, *18*(1), 193–222.
- Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human brain mapping*, 15(2), 95–111.
- 45. Diano, M., Celeghin, A., Bagnis, A., & Tamietto, M. (2017). Amygdala response to emotional stimuli without awareness: facts and interpretations. *Frontiers in Psychology*, 7, 234677.
- 46. Dou, H., Liang, L., Ma, J., Lu, J., Zhang, W., & Li, Y. (2021). Irrelevant task suppresses the N170 of automatic attention allocation to fearful faces. *Scientific Reports*, *11*(1), 11754.
- 47. Dux, P. E., & Marois, R. (2009). The attentional blink: A review of data and theory. *Attention, Perception, & Psychophysics*, 71(8), 1683–1700.
- 48. Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, *11*(10), 2319-2324.
- 49. Eimer, M., & Kiss, M. (2007). Attentional capture by task-irrelevant fearful faces is revealed by the N2pc component. *Biological psychology*, 74(1), 108–112.
- Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of cognitive neuroscience*, 20(8), 1423–1433.
- 51. Eklund, R., & Wiens, S. (2018). Visual awareness negativity is an early neural correlate of awareness: A preregistered study with two Gabor sizes. *Cognitive, Affective, & Behavioral Neuroscience, 18*(1), 176–188.
- Esteves, F., Dimberg, U., & Öhman, A. (1994). Automatically elicited fear: Conditioned skin conductance responses to masked facial expressions. *Cognition & Emotion*, 8(5), 393–413.
- 53. Faivre, N., & Kouider, S. (2011). Multi-feature objects elicit nonconscious priming despite crowding. *Journal of Vision*, *11*(3), 2–2.

- 54. Faivre, N., Dubois, J., Schwartz, N., & Mudrik, L. (2019). Imaging object-scene relations processing in visible and invisible natural scenes. *Scientific reports*, 9(1), 4567.
- 55. Förster, J., Koivisto, M., & Revonsuo, A. (2020). ERP and MEG correlates of visual consciousness: The second decade. *Consciousness and Cognition*, *80*, 102917.
- 56. Fox, E. (2002). Processing emotional facial expressions: The role of anxiety and awareness. *Cognitive, Affective, & Behavioral Neuroscience, 2*(1), 52–63.
- 57. Furtak, M., Doradzińska, Ł., Ptashynska, A., Mudrik, L., Nowicka, A., & Bola, M. (2020). Automatic attention capture by threatening, but not by semantically incongruent natural scene images. *Cerebral Cortex*, *30*(7), 4158–4168.
- 58. Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences*, 96(6), 3314–3319.
- 59. Garrido, M. I., Barnes, G. R., Sahani, M., & Dolan, R. J. (2012). Functional evidence for a dual route to amygdala. *Current Biology*, 22(2), 129–134.
- 60. Gareze, L., & Findlay, J. M. (2007). Absence of scene context effects in object detection and eye gaze capture. In *Eye Movements* (pp. 617–637). Elsevier.
- 61. Gerdes, A. B., & Alpers, G. W. (2014). You see what you fear: spiders gain preferential access to conscious perception in spider-phobic patients. *Journal of Experimental Psychopathology*, 5(1), 14–28.
- 62. Gläscher, J., & Adolphs, R. (2003). Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. *Journal of Neuroscience*, 23(32), 10274–10282.
- 63. Goldstein, A., & Hassin, R. R. (2017). Commentary: Definitely maybe: can unconscious processes perform the same functions as conscious processes?. *Frontiers in Psychology*, *8*, 229617.
- 64. Grassini, S., Holm, S. K., Railo, H., & Koivisto, M. (2016). Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. *Biological Psychology*, *121*, 53–61.
- 65. Graziano, M. S. (2022). A conceptual framework for consciousness. *Proceedings of the National Academy of Sciences*, *119*(18), e2116933119.
- 66. Gupta, R. S., Kujawa, A., & Vago, D. R. (2019). The neural chronometry of threat-related attentional bias: Event-related potential (ERP) evidence for early and late stages of selective attentional processing. *International Journal of Psychophysiology*, *146*, 20–42.

- 67. Hajcak, G., MacNamara, A., & Olvet, D. M. (2010). Event-related potentials, emotion, and emotion regulation: an integrative review. *Developmental neuropsychology*, *35*(2), 129–155.
- 68. Hamm, A. O., Schupp, H. T., & Weike, A. I. (2003). Motivational organization of emotions: Autonomic changes, cortical responses, and reflex modulation. *Handbook of affective sciences*, 187–211.
- 69. Hassin, R. R. (2013). Yes it can: On the functional abilities of the human unconscious. *Perspectives on Psychological Science*, 8(2), 195–207.
- 70. Hedger, N., Adams, W. J., & Garner, M. (2015). Autonomic arousal and attentional orienting to visual threat are predicted by awareness. *Journal of Experimental Psychology: Human perception and performance*, 41(3), 798.
- Hedger, N., Gray, K. L., Garner, M., & Adams, W. J. (2016). Are visual threats prioritized without awareness? A critical review and meta-analysis involving 3 behavioral paradigms and 2696 observers. *Psychological bulletin*, 142(9), 934.
- 72. Hedger, N., Garner, M., & Adams, W. J. (2019). Do emotional faces capture attention, and does this depend on awareness? Evidence from the visual probe paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, 45(6), 790.
- 73. Hein, E., Rolke, B., & Ulrich, R. (2006). Visual attention and temporal discrimination: Differential effects of automatic and voluntary cueing. *Visual Cognition*, *13*(1), 29–50.
- 74. Henderson, J. M., Weeks, P. A., Jr, & Hollingworth, A. (1999). The effects of semantic consistency on eye movements during complex scene viewing. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(1), 210.
- Henderson, J. M., Williams, C. C., Castelhano, M. S., & Falk, R. J. (2003). Eye movements and picture processing during recognition. *Perception & psychophysics*, 65(5), 725–734.
- Henderson, J. M., & Pierce, G. L. (2008). Eye movements during scene viewing: Evidence for mixed control of fixation durations. *Psychonomic Bulletin & Review*, 15, 566–573.
- 77. Hesselmann, G., & Moors, P. (2015). Definitely maybe: can unconscious processes perform the same functions as conscious processes?. *Frontiers in Psychology*, *6*, 145300.
- Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353(1373), 1257–1270.

- 79. Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, 55, 498–509.
- 80. Hirschhorn, R., Kahane, O., Gur-Arie, I., Faivre, N., & Mudrik, L. (2021). Windows of integration hypothesis revisited. *Frontiers in Human Neuroscience*, *14*, 617187.
- 81. Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Cognitive Brain Research*, *16*(2), 174–184.
- 82. Hollingworth, A., & Henderson, J. M. (2000). Semantic informativeness mediates the detection of changes in natural scenes. *Visual Cognition*, 7(1-3), 213–235.
- 83. Hsieh, P. J., Colas, J. T., & Kanwisher, N. (2011). Unconscious pop-out: Attentional capture by unseen feature singletons only when top-down attention is available. *Psychological Science*, 22(9), 1220.
- 84. James, W. (1890). The principles of psychology (Vol. 1). H. Holt and company.
- 85. Jeffreys, D. A., & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked potentials. I. Component of striate cortical origin. *Experimental brain research*, *16*, 1–21.
- Jehee, J. F., Brady, D. K., & Tong, F. (2011). Attention improves encoding of task-relevant features in the human visual cortex. *Journal of Neuroscience*, 31(22), 8210–8219.
- Jiang, Y. I., Shannon, R. W., Vizueta, N., Bernat, E. M., Patrick, C. J., & He, S. (2009). Dynamics of processing invisible faces in the brain: Automatic neural encoding of facial expression information. *Neuroimage*, 44(3), 1171–1177.
- 88. Jiang, Y., Wu, X., Saab, R., Xiao, Y., & Gao, X. (2018). Time course of influence on the allocation of attentional resources caused by unconscious fearful faces. *Neuropsychologia*, *113*, 104–110.
- Jolicœur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–172.
- 90. Kaiser, D., Quek, G. L., Cichy, R. M., & Peelen, M. V. (2019). Object vision in a structured world. *Trends in Cognitive Sciences*, 23(8), 672–685.
- 91. Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, 3(8), 759–763.
- 92. Kanwisher, N., & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2109–2128.

- 93. Kentridge, R. W. (2011). Attention without awareness. *Attention: Philosophical and psychological essays*, 228.
- 94. Kinchla, R. A. (1980). The measurement of attention. In *Attention and Performance VIII* (pp. 213-238). Psychology Press.
- 95. Kiss, M., & Eimer, M. (2008). ERPs reveal subliminal processing of fearful faces. *Psychophysiology*, 45(2), 318–326.
- 96. Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends in cognitive sciences*, *11*(1), 16–22.
- 97. Koivisto, M., Revonsuo, A., & Salminen, N. (2005). Independence of visual awareness from attention at early processing stages. *NeuroReport*, *16*(8), 817.
- Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006). Independence of Visual Awareness from the Scope of Attention: An Electrophysiological Study. *Cerebral Cortex*, 16(3), 415–424.
- 99. Koivisto, M., & Revonsuo, A. (2007). Electrophysiological correlates of visual consciousness and selective attention. *NeuroReport*, 18(8), 753.
- 100. Koivisto, M., Lähteenmäki, M., Sørensen, T. A., Vangkilde, S., Overgaard, M., & Revonsuo, A. (2008). The earliest electrophysiological correlate of visual awareness? *Brain and Cognition*, 66(1), 91–103.
- 101. Koivisto, M., & Revonsuo, A. (2008). The role of selective attention in visual awareness of stimulus features: Electrophysiological studies. *Cognitive, Affective, & Behavioral Neuroscience*, 8(2), 195–210.
- 102. Koivisto, M., Kainulainen, P., & Revonsuo, A. (2009). The relationship between awareness and attention: Evidence from ERP responses. *Neuropsychologia*, 47(13), 2891–2899.
- 103. Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience & Biobehavioral Reviews*, *34*(6), 922–934.
- 104. Koivisto, M., & Grassini, S. (2016). Neural processing around 200 ms after stimulus-onset correlates with subjective visual awareness. *Neuropsychologia*, 84, 235–243.
- 105. Koster, E. H., Verschuere, B., Burssens, B., Custers, R., & Crombez, G. (2007). Attention for emotional faces under restricted awareness revisited: do emotional faces automatically attract attention?. *Emotion*, 7(2), 285.
- 106. Kowler, E. (2011). Eye movements: The past 25 years. Vision Research, 51(13), 1457–1483.

- Lähteenmäki, M., Hyönä, J., Koivisto, M., & Nummenmaa, L. (2015). Affective processing requires awareness. *Journal of Experimental Psychology: General*, 144(2), 339.
- 108. Lamme, V. A. F. (2000). Neural Mechanisms of Visual Awareness: A Linking Proposition. *Brain and Mind*, 1(3), 385–406.
- 109. Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23(11), 571–579.
- 110. Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7(1), 12–18.
- 111. Lamme, V. A. F. (2004). Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks*, *17*(5), 861–872.
- 112. Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501
- 113. Lamy, D., & Egeth, H. E. (2003). Attentional capture in singleton-detection and feature-search modes. *Journal of Experimental Psychology: Human Perception and Performance*, 29(5), 1003.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. *Technical Report* A-8. University of Florida, Gainesville, FL.
- LaPointe, M. R., Lupianez, J., & Milliken, B. (2013). Context congruency effects in change detection: Opposing effects on detection and identification. *Visual Cognition*, 21(1), 99–122.
- 116. LeDoux, J. E. (1998). *The emotional brain: The mysterious underpinnings of emotional life*. Simon and Schuster.
- 117. LeDoux, J. (2012). Rethinking the emotional brain. Neuron, 73(4), 653-676.
- 118. LeDoux, J. E., & Brown, R. (2017). A higher-order theory of emotional consciousness. *Proceedings of the National Academy of Sciences*, *114*(10), E2016–E2025.
- 119. Lennie, P. (2003). The cost of cortical computation. Current Biology, 13(6), 493–497.
- 120. Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. *Journal of cognitive neuroscience*, *16*(3), 479–486.
- 121. Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., ... & Williams, L. M. (2005). A direct brainstem–amygdala–cortical 'alarm'system for subliminal signals of fear. *Neuroimage*, 24(1), 235–243.

- 122. Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research*, *46*(8-9), 1210–1220.
- 123. Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-based attention modulates orientation-selective responses in human visual cortex. *Neuron*, *55*(2), 313–323.
- 124. Loftus, G. R., & Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. *Journal of Experimental Psychology: Human perception and performance*, 4(4), 565.
- 125. Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20(5), 1000.
- 126. Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77(1), 24–42.
- 127. Luck, S. J., & Kappenman, E. S. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. *The Oxford handbook of event-related potential components*, 329–360.
- 128. Luck, S. J., & Kappenman, E. S. (Eds.). (2013). *The Oxford handbook of event-related potential components*. Oxford University Press.
- 129. Luck, S. J. (2014). An introduction to the event-related potential technique. MIT Press.
- 130. Mack, A., & Rock, I. (1998). Inattentional blindness: Perception without attention. *Visual attention*, 8(01).
- 131. Mack, A., Clarke, J., Erol, M., & Bert, J. (2017). Scene incongruity and attention. *Consciousness and Cognition*, 48, 87–103.
- 132. MacNamara, A., Kappenman, E. S., Black, S. R., Bress, J. N., & Hajcak, G. (2013). 11 integrating behavioral and electrocortical measures of attentional bias toward threat. In *Handbook of self-regulatory processes in development* (pp. 215–243). Psychology Press.
- 133. Maier, A., & Tsuchiya, N. (2021). Growing evidence for separate neural mechanisms for attention and consciousness. *Attention, perception, & psychophysics, 83, 558-576.*
- 134. Maratos, F. A., Mogg, K., & Bradley, B. P. (2008). Identification of angry faces in the attentional blink. *Cognition and Emotion*, 22(7), 1340–1352.
- 135. Marchewka, A., Żurawski, Ł., Jednoróg, K., & Grabowska, A. (2014). The Nencki Affective Picture System (NAPS): Introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior research methods*, *46*, 596–610.

- Martínez, A., Teder-Sälejärvi, W., Vazquez, M., Molholm, S., Foxe, J. J., Javitt, D. C.,
 ... & Hillyard, S. A. (2006). Objects are highlighted by spatial attention. *Journal of cognitive neuroscience*, 18(2), 298–310.
- 137. McAdams, C. J., & Reid, R. C. (2005). Attention modulates the responses of simple cells in monkey primary visual cortex. *Journal of Neuroscience*, *25*(47), 11023–11033.
- 138. McAlonan, K., Cavanaugh, J., & Wurtz, R. H. (2008). Guarding the gateway to cortex with attention in visual thalamus. *Nature*, *456*(7220), 391–394.
- McMains, S. A., Fehd, H. M., Emmanouil, T. A., & Kastner, S. (2007). Mechanisms of feature-and space-based attention: response modulation and baseline increases. *Journal* of *Neurophysiology*, 98(4), 2110–2121.
- 140. Melnikoff, D. E., & Bargh, J. A. (2018). The mythical number two. *Trends in cognitive sciences*, 22(4), 280-293.
- 141. Milders, M., Sahraie, A., Logan, S., & Donnellon, N. (2006). Awareness of faces is modulated by their emotional meaning. *Emotion*, 6(1), 10.
- Mogg, K., & Bradley, B. P. (1999). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition & Emotion*, 13(6), 713–740.
- 143. Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual review of psychology, 68,* 47–72.
- 144. Moors, P., Boelens, D., Van Overwalle, J., & Wagemans, J. (2016). Scene integration without awareness: No conclusive evidence for processing scene congruency during continuous flash suppression. *Psychological Science*, *27*(7), 945–956.
- 145. Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229(4715), 782–784.
- 146. Morey, R. D. (2008). Confidence intervals from normalized data: A correction to Cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, 4(2), 61-64.
- 147. Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences*, 96(4), 1680–1685.
- 148. Mudrik, L., Lamy, D., & Deouell, L. Y. (2010). ERP evidence for context congruity effects during simultaneous object-scene processing. *Neuropsychologia*, 48(2), 507–517.
- 149. Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration without awareness: Expanding the limits of unconscious processing. *Psychological science*, 22(6), 764–770.

- 150. Mudrik, L., Faivre, N., & Koch, C. (2014). Information integration without awareness. *Trends in cognitive sciences*, *18*(9), 488–496.
- 151. Mudrik, L., & Deouell, L. Y. (2022). Neuroscientific evidence for processing without awareness. *Annual review of neuroscience*, 45, 403–423.
- 152. Muller, H. J. PM (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15(2).
- 153. Naccache, L., Blandin, E., & Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychological science*, *13*(5), 416–424.
- 154. Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*(11), 1631–1647.
- 155. Nakayama, K., & Martini, P. (2011). Situating visual search. Vision Research, 51(13), 1526–1537.
- 156. Natale, E., Marzi, C. A., Girelli, M., Pavone, E. F., & Pollmann, S. (2006). ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *European Journal of Neuroscience*, 23(9), 2511–2521.
- 157. Neisser, U. (1967) Cognitive psychology Appleton Century Crofts
- 158. Öhman, A., Carlsson, K., Lundqvist, D., & Ingvar, M. (2007). On the unconscious subcortical origin of human fear. *Physiology & behavior*, 92(1-2), 180–185.
- 159. Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: an integrative review of ERP findings. *Biological psychology*, 77(3), 247–265.
- 160. O'regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and brain sciences*, 24(5), 939–973.
- 161. Ortiz-Tudela, J., Milliken, B., Botta, F., LaPointe, M., & Lupianez, J. (2017). A cow on the prairie vs. a cow on the street: Long-term consequences of semantic conflict on episodic encoding. *Psychological Research*, *81*, 1264–1275.
- 162. Ortiz-Tudela, J., Martín-Arévalo, E., Chica, A. B., & Lupiáñez, J. (2018). Semantic incongruity attracts attention at a pre-conscious level: Evidence from a TMS study. *Cortex*, 102, 96–106.
- 163. Peelen, M. V., & Kastner, S. (2014). Attention in the real world: toward understanding its neural basis. *Trends in cognitive sciences*, *18*(5), 242–250.
- 164. Pegna, A. J., Khateb, A., Lazeyras, F., & Seghier, M. L. (2005). Discriminating emotional faces without primary visual cortices involves the right amygdala. *Nature Neuroscience*, 8(1), 24–25.

- Pegna, A. J., Landis, T., & Khateb, A. (2008). Electrophysiological evidence for early non-conscious processing of fearful facial expressions. *International Journal of Psychophysiology*, 70(2), 127–136.
- 166. Pegna, A. J., Darque, A., Berrut, C., & Khateb, A. (2011). Early ERP modulation for task-irrelevant subliminal faces. *Frontiers in Psychology*, *2*, 9489.
- 167. Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy* of Sciences, 99(17), 11458–11463.
- Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *Journal of Neuroscience*, 23(10), 3990–3998.
- 169. Pessoa, L., Japee, S., & Ungerleider, L. G. (2005). Visual awareness and the detection of fearful faces. *Emotion*, 5(2), 243.
- 170. Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, 11(11), 773–782.
- 171. Phelps, E. A. (2006). Emotion and cognition: insights from studies of the human amygdala. *Annu. Rev. Psychol.*, 57, 27–53.
- 172. Pitts, M. A., Metzler, S., & Hillyard, S. A. (2014). Isolating neural correlates of conscious perception from neural correlates of reporting one's perception. *Frontiers in Psychology*, *5*.
- 173. Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148.
- 174. Polich, J. (2012). Neuropsychology of P300. The Oxford handbook of event-related potential components, 641, 159-188.
- 175. Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of experimental psychology: General*, 109(2), 160.
- 176. Posner, M. I., Inhoff, A. W., Friedrich, F. J., & Cohen, A. (1987). Isolating attentional systems: A cognitive-anatomical analysis. *Psychobiology*, *15*(2), 107–121.
- 177. Posner, M. I. (1994). Attention: the mechanisms of consciousness. *Proceedings of the National Academy of Sciences*, *91*(16), 7398–7403.
- 178. Qiu, Z., Becker, S. I., & Pegna, A. J. (2022a). Spatial attention shifting to emotional faces is contingent on awareness and task relevancy. *Cortex*, *151*, 30–48.

- 179. Qiu, Z., Becker, S. I., & Pegna, A. J. (2022b). Spatial attention shifting to fearful faces depends on visual awareness in attentional blink: An ERP study. *Neuropsychologia*, 172, 108283.
- 180. Qiu, Z., Zhang, J., & Pegna, A. J. (2023). Neural processing of lateralised task-irrelevant fearful faces under different awareness conditions. *Consciousness and Cognition*, 107, 103449.
- 181. Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition*, 20(3), 972–983.
- 182. Rayner, K., Castelhano, M. S., & Yang, J. (2009). Eye movements when looking at unusual/weird scenes: Are there cultural differences? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 35*(1), 254.
- 183. Remington, R. W., Johnston, J. C., & Yantis, S. (1992). Involuntary attentional capture by abrupt onsets. *Perception & Psychophysics*, *51*(3), 279–290.
- 184. Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annu. Rev. Neurosci.*, 27, 611–647.
- 185. Richler, J. J., Wong, Y. K., & Gauthier, I. (2011). Perceptual expertise as a shift from strategic interference to automatic holistic processing. *Current directions in psychological science*, 20(2), 129–134.
- 186. Riegel, M., Żurawski, Ł., Wierzba, M., Moslehi, A., Klocek, Ł., Horvat, M., ... & Marchewka, A. (2016). Characterization of the Nencki Affective Picture System by discrete emotional categories (NAPS BE). *Behavior research methods*, 48, 600–612.
- 187. Ritchie, K. L., Bannerman, R. L., & Sahraie, A. (2011). The effect of fear in the periphery in binocular rivalry. *Perception*, 40(12), 1395–1401.
- 188. Roelfsema, P. R., Lamme, V. A., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, *395*(6700), 376–381.
- 189. Rosa, P. J., Esteves, F., & Arriaga, P. (2014, June). Effects of fear-relevant stimuli on attention: integrating gaze data with subliminal exposure. In 2014 IEEE International Symposium on Medical Measurements and Applications (MeMeA) (pp. 1–6). IEEE.
- 190. Rosenthal, D. M. (2008). Consciousness and its function. *Neuropsychologia*, 46(3), 829–840.
- 191. Ruiz-Padial, E., Mata, J. L., Rodríguez, S., Fernández, M. C., & Vila, J. (2005). Non-conscious modulation of cardiac defense by masked phobic pictures. *International journal of psychophysiology*, 56(3), 271–281.

- 192. Schindler, S., & Bublatzky, F. (2020). Attention and emotion: An integrative review of emotional face processing as a function of attention. *Cortex*, *130*, 362–386.
- 193. Schlossmacher, I., Junghöfer, M., Straube, T., & Bruchmann, M. (2017). No differential effects to facial expressions under continuous flash suppression: An event-related potentials study. *NeuroImage*, *163*, 276–285.
- 194. Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion*, 4(2), 189.
- 195. Sessa, P., Luria, R., Gotler, A., Jolicœur, P., & Dell'Acqua, R. (2011). Interhemispheric ERP asymmetries over inferior parietal cortex reveal differential visual working memory maintenance for fearful versus neutral facial identities. *Psychophysiology*, 48(2), 187–197.
- 196. Shafto, J. P., & Pitts, M. A. (2015). Neural Signatures of Conscious Face Perception in an Inattentional Blindness Paradigm. *Journal of Neuroscience*, *35*(31), 10940–10948.
- 197. Shapiro, K. L., Raymond, J. E., & Arnell, K. M. (1997). The attentional blink. *Trends in cognitive sciences*, *1*(8), 291–296.
- 198. Shir, Y., Abudarham, N., & Mudrik, L. (2021). You won't believe what this guy is doing with the potato: The ObjAct stimulus-set depicting human actions on congruent and incongruent objects. *Behavior Research Methods*, 1–15.
- 199. Silvert, L., Lepsien, J., Fragopanagos, N., Goolsby, B., Kiss, M., Taylor, J. G., ... & Nobre, A. C. (2007). Influence of attentional demands on the processing of emotional facial expressions in the amygdala. *Neuroimage*, 38(2), 357–366.
- 200. Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in cognitive sciences*, *1*(7), 261–267.
- 201. Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception*, *28*(9), 1059–1074.
- 202. Simons, D. J., & Rensink, R. A. (2005). Change blindness: Past, present, and future. *Trends in cognitive sciences*, 9(1), 16–20.
- 203. Soltani, A., & Koch, C. (2010). Visual saliency computations: mechanisms, constraints, and the effect of feedback. *Journal of Neuroscience*, *30*(38), 12831–12843.
- 204. Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences*, *96*(4), 1663–1668.

- 205. Stewart, L. H., Ajina, S., Getov, S., Bahrami, B., Todorov, A., & Rees, G. (2012). Unconscious evaluation of faces on social dimensions. *Journal of Experimental Psychology: General*, 141(4), 715.
- 206. Szczepanowski, R., & Pessoa, L. (2007). Fear perception: can objective and subjective awareness measures be dissociated?. *Journal of Vision*, 7(4), 10–10.
- 207. Tamietto, M., Castelli, L., Vighetti, S., Perozzo, P., Geminiani, G., Weiskrantz, L., & de Gelder, B. (2009). Unseen facial and bodily expressions trigger fast emotional reactions. *Proceedings of the National Academy of Sciences*, 106(42), 17661–17666.
- 208. Tamietto, M., & De Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, *11*(10), 697–709.
- 209. Tamietto, M., Cauda, F., Celeghin, A., Diano, M., Costa, T., Cossa, F. M., ... & de Gelder, B. (2015). Once you feel it, you see it: insula and sensory-motor contribution to visual awareness for fearful bodies in parietal neglect. *Cortex*, 62, 56–72.
- Tipura, E., & Pegna, A. J. (2022). Subliminal emotional faces do not capture attention under high attentional load in a randomized trial presentation. *Visual Cognition*, 30(4), 280–288.
- 211. Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., ... & Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry research*, 168(3), 242–249.
- 212. Treisman, A. M. (1960). Contextual cues in selective listening. *Quarterly Journal of Experimental Psychology*, 12(4), 242–248.
- 213. Troiani, V., Price, E. T., & Schultz, R. T. (2014). Unseen fearful faces promote amygdala guidance of attention. *Social Cognitive and Affective Neuroscience*, 9(2), 133–140.
- 214. Underwood, G., & Foulsham, T. (2006). Visual saliency and semantic incongruency influence eye movements when inspecting pictures. *The Quarterly Journal of Experimental Psychology*, *59*(11), 1931–1949.
- 215. Underwood, G., Humphreys, L., & Cross, E. (2007). Congruency, saliency and gist in the inspection of objects in natural scenes. In *Eye Movements* (pp. 563-VII). Elsevier.
- 216. Underwood, G., Templeman, E., Lamming, L., & Foulsham, T. (2008). Is attention necessary for object identification? Evidence from eye movements during the inspection of real-world scenes. *Consciousness and Cognition*, 17(1), 159–170.
- 217. Van Der Lubbe, R. H., Neggers, S. F., Verleger, R., & Kenemans, J. L. (2006). Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. *Brain Research*, *1072*(1), 133–152.

- 218. van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., & Verbaten, R. (1998). Baseline salivary cortisol levels and preconscious selective attention for threat: A pilot study. *Psychoneuroendocrinology*, 23(7), 741–747.
- 219. van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., & Verbaten, R. (2000). Conscious and preconscious selective attention to social threat: Different neuroendocrine response patterns. *Psychoneuroendocrinology*, 25(6), 577–591.
- 220. Van Hooff, J. C., Devue, C., Vieweg, P. E., & Theeuwes, J. (2013). Disgust-and not fear-evoking images hold our attention. *Acta Psychologica*, 143(1), 1–6.
- 221. Van Hooff, J. C., van Buuringen, M., El M'rabet, I., de Gier, M., & van Zalingen, L. (2014). Disgust-specific modulation of early attention processes. *Acta Psychologica*, 152, 149–157.
- 222. Võ, M. L. H., & Henderson, J. M. (2009). Does gravity matter? Effects of semantic and syntactic inconsistencies on the allocation of attention during scene perception. *Journal of Vision*, *9*(3).
- 223. Võ, M. L. H., & Henderson, J. M. (2011). Object-scene inconsistencies do not capture gaze: Evidence from the flash-preview moving-window paradigm. *Attention, Perception, & Psychophysics*, 73(6), 1742–1753.
- 224. Võ, M. L. H., Boettcher, S. E., & Draschkow, D. (2019). Reading scenes: How scene grammar guides attention and aids perception in real-world environments. *Current Opinion in Psychology*, 29, 205–210.
- 225. Wang, L., Feng, C., Mai, X., Jia, L., Zhu, X., Luo, W., & Luo, Y. J. (2016). The impact of perceptual load on the non-conscious processing of fearful faces. *Plos one*, *11*(5), e0154914.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, 18(1), 411–418.
- Williams, L. M., Brown, K. J., Das, P., Boucsein, W., Sokolov, E. N., Brammer, M. J., ... & Gordon, E. (2004a). The dynamics of cortico-amygdala and autonomic activity over the experimental time course of fear perception. *Cognitive Brain Research*, 21(1), 114–123.
- 228. Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004b). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *Journal of Neuroscience*, 24(12), 2898–2904.
- 229. Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., ... & Gordon, E. (2004c). Mapping the time course of nonconscious and conscious

perception of fear: an integration of central and peripheral measures. *Human brain mapping*, 21(2), 64–74.

- 230. Wolfe, J. M., & Horowitz, T. S. (2017). Five factors that guide attention in visual search. *Nature Human Behaviour*, 1(3), 0058.
- 231. Womelsdorf, T., & Fries, P. (2007). The role of neuronal synchronization in selective attention. *Current opinion in neurobiology*, 17(2), 154–160.
- 232. Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 29(1), 121.
- 233. Wójcik, M. J., Nowicka, M. M., Bola, M., & Nowicka, A. (2019). Unconscious detection of one's own image. *Psychological science*, *30*(4), 471–480.
- 234. Wu, C. C., Wick, F. A., & Pomplun, M. (2014). Guidance of visual attention by semantic information in real-world scenes. *Frontiers in Psychology*, *5*, 54.
- 235. Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*, 7(4), 882.
- 236. Yokoyama, T., Noguchi, Y., & Kita, S. (2013). Unconscious processing of direct gaze: Evidence from an ERP study. *Neuropsychologia*, *51*(7), 1161–1168.
- 237. Zivony, A., Allon, A. S., Luria, R., & Lamy, D. (2018). Dissociating between the N2pc and attentional shifting: An attentional blink study. *Neuropsychologia*, *121*, 153–163.
- 238. Zotto, M. D., & Pegna, A. J. (2015). Processing of masked and unmasked emotional faces under different attentional conditions: An electrophysiological investigation. *Frontiers in Psychology*, 6.

Publication 1

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CO-AUTHOR'S STATEMENT

As the first author of the article:

Doradzińska, Ł., Furtak, M., & Bola, M. (2022). Perception of semantic relations in scenes: A registered report study of attention hold. *Consciousness and Cognition, 100*, 103315.

I declare that my contribution to this publication included:

- participation in the development of the research concept

- critical analysis of existing literature
- development of the experimental procedure
- preparation of PRESENTATION scripts for the presentation of visual stimuli which

included stimulus sequence randomization

- preparation of PYTHON scripts used for behavioral data analysis

- selection of statistical tools suitable for data analysis
- analysis of behavioral data
- interpretation and discussion of obtained results
- preparation of the initial version of the manuscript
- preparation of most of the figures included in the publication
- participation in correcting and complementing the final version of the manuscript

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I declare that my contribution to this publication included:

- consultation on experimental design

- selection of visual stimuli and analysis of their features (emotional valence and arousal, luminance, contrast)

- recruitment of participants and superintending experimental procedure

- consultation on the interpretations of obtained results

- preparation of one figure included in the manuscript

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I declare that this publication was prepared as a part of the OPUS NCN grant I managed (2018/29/B/HS6/02152). My contribution to the publication included establishing the research concept, substantive supervision, consulting the experimental procedure and the interpretation of obtained results, and correcting the final version of the manuscript.

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Perception of semantic relations in scenes: A registered report study of attention hold



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ABSTRACT

To what extent the semantic relations present in scenes guide spatial attention automatically remains a matter of debate. Considering that spatial attention can be understood as a sequence of shifts, engagements, and disengagements, semantic relations might affect each stage of this process differently. Therefore, we investigated whether objects that violate semantic rules engage attention for longer than objects that are expected in a given context. The experiment involved a central presentation of a distractor scene that contained a semantically congruent or incongruent object, and a peripheral presentation of a small target letter. We found that incongruent scenes did not delay responses to the peripheral target, which indicates that they did not hold attention for longer than congruent scenes. Therefore, by showing that violations of semantic relations do not engage attention automatically, our study contributes to a better understanding of how attention operates in naturalistic settings.

1. Introduction

A scene can be defined as a view of the environment that comprises both background elements and discrete objects, all arranged according to certain spatial and semantic rules (Henderson and Hollingworth, 1999). Thus, in real-world scenes, objects always occur in relation to other scene elements, and these relations (both spatial and semantic) play a key role in the object recognition process (Bar, 2004; Kaiser et al., 2019; Võ et al., 2019). This role has been convincingly shown by studies investigating perception of semantically incongruent objects, which are defined as those with a very low probability of occurring in a given context and which therefore violate observers' expectations regarding a scene's composition (Biederman et al., 1982). A robust body of evidence indicates that semantically incongruent objects are recognized more slowly and less accurately than congruent ones (Boyce et al. 1989; Davenport and Potter 2004; Rieger et al. 2008; Leroy et al., 2020; Furtak et al., 2022). These findings are taken as evidence that contextual information in the form of gist or global scene statistics is computed first, and that it facilitates subsequent recognition of congruent objects by pre-activating their representations (Hochstein and Ahissar, 2002; Bar, 2004; Oliva and Torralba, 2006).

Contextual information is also known to guide further exploration of a scene by directing spatial attention to locations and objects expected to be most informative (Peelen and Kastner, 2014; Wu et al., 2014; Kaiser et al., 2019; Wolfe and Horowitz, 2017; Võ et al., 2019). In line with the assumption that unexpected stimuli are most informative, some studies have found that incongruent objects attract attention automatically. For instance, participants directed their initial saccades to incongruent objects in eye-tracking studies (Loftus and Mackworth 1978; Underwood and Foulsham 2006; Becker et al. 2007; Underwood et al. 2007, 2008; Bonitz and Gordon

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Received 2 November 2021; Received in revised form 7 March 2022; Accepted 12 March 2022 Available online 24 March 2022 1053-8100/© 2022 Elsevier Inc. All rights reserved. 2008) and detected a change more quickly if a scene contained an incongruent object in the change-blindness paradigm (Hollingworth and Henderson 2000; LaPointe et al. 2013; Mack et al. 2017; LaPointe and Milliken 2017; Ortiz-Tudela et al. 2017, 2018). If confirmed, this would suggest that semantic relations in real-world scenes are analyzed pre-attentively and are used to guide the deployment of spatial attention. However, numerous other studies did not find evidence supporting automatic attention capture by incongruent objects (e.g., De Graef et al. 1990; Gareze and Findlay 2007; Rayner et al. 2009; Vo and Henderson 2009, 2011; Cornelissen and Vo 2017). Therefore, we recently conducted a study in order to address this controversy (Furtak et al., 2020). To provide conclusive evidence for or against automatic attention capture by incongruent objects, the aforementioned study was designed in the following way. First, we employed a set of congruent and incongruent scene images which had been validated in several previous studies (Mudrik et al. 2010, 2011, 2014; Moors et al., 2016; Mack et al., 2017; Biderman and Mudrik 2018; Faivre et al. 2019; Shir et al., 2021). Second, we employed a well-established methodology based on the dot-probe task and N2pc ERP component analysis that has been used to investigate attention capture by threatening real-world scenes (Kappenman et al., 2014, 2015). Third, we also included the threatening scene images from the study by Kappenman and colleagues in a 'positive control' condition in our experiment. These steps were taken to strengthen our conclusions, particularly in the case of a null result in the incongruent condition (i.e., no attention capture). Specifically, we reasoned that demonstrating attention capture caused by threatening scenes in the "positive control" condition of our experiment would mitigate the concern that our procedure was not sensitive enough, or concerns about any other general factors that potentially explain the lack of the effect in the incongruent scenes would also be mitigated. This was indeed what we found: we replicated the original result of Kappenman and colleagues (2015) by showing that threatening images did attract attention; however, we found no evidence for attention shifts to semantically incongruent scenes.

Even though our study demonstrated that incongruent objects did not capture attention automatically (Furtak et al., 2020), such objects might still be prioritized by attention in other ways. The classic theory of attention proposed by Posner and colleagues (1987) differentiates two independent functionalities of spatial attention orienting: attention shifts, defined as 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 and shift to a new one. Two lines of research have suggested that semantically incongruent objects engage and hold attention for longer than congruent ones. First, eye-tracking studies have demonstrated that participants fixate on incongruent objects more frequently and for longer in comparison to congruent ones when they are exploring a scene freely (Vo and Henderson, 2009, 2011). However, in eye-tracking studies, covert attention orienting cannot be dissociated from overt eye movements (e.g., Hunt and Kingstone, 2003; Juan et al., 2004), which prevents identification of the specific mechanisms that contribute to longer fixations. Moreover, in these previous eye-tracking studies, participants were allowed to explore a scene freely and for a relatively long time, thus it is not known to what extent the effect was indeed automatic and involuntary (but see Cornelissen and Vo, 2017). Second, in the binocular rivalry paradigm, incongruent objects did not enter awareness preferentially, but once they were perceived, their dominance lasted longer (Mudrik et al., 2011). Yet, while such an observation indicates greater involvement of attentional resources in the processing of incongruent objects, it does not inform us about spatial attention orienting (i.e., patterns of shifts and engagements). Therefore, whether or not semantically incongruent objects hold spatial attention requires further study.

The holding of spatial attention can be specifically measured using a paradigm that involves simultaneous presentations of a central distractor image and a peripheral target stimulus. It can be inferred that the central distractor holds attention if a response to the target is delayed. Such a paradigm has been used in several previous studies. For instance, when a centrally presented simple distractor shape exhibits task-relevant features (i.e., the same color as a target), it holds attention and delays shifts to a peripheral target stimulus (Folk et al., 2009; but see Zivony & Lamy, 2014). Additionally, faces are considered to benefit from general attentional prioritization and, indeed, a face image displayed centrally delays reaction to a peripheral target in comparison to images of other non-face stimuli (Bindemann et al., 2005). Finally, two studies conducted by van Hoff and colleagues (2013, 2014) found that disgust-evoking images hold attention and impair recognition of peripherally presented letters. The effect was specific to disgust-evoking images, as other emotional categories, such as fear, sadness, or happiness, did not cause a similar effect.

The present study tested the hypothesis that semantically incongruent objects hold spatial attention for longer than congruent ones. To provide robust evidence in favor of either the null or the alternative hypothesis, the study was guided by the same logic as our previous work on attention capture (Furtak et al., 2020). First, we used the scene images developed by Mudrik et al. (2010), which made it possible to compare the results of the present study to the previous work of our and other groups using the same stimuli set (e. g., Mudrik et al. 2011, 2014; Moors et al., 2016; Mack et al., 2017; Biderman and Mudrik 2018; Faivre et al. 2019; Furtak et al., 2020; Shir et al., 2021). Second, we employed a procedure developed specifically to investigate automatic holding of spatial attention by real-world scene images (van Hooff et al., 2013, 2014). Third, to establish a 'positive control' condition, we included disgust-evoking images in our study and aimed to replicate the main result of van Hooff and colleagues (2014). Successful replication would indicate that the paradigm established in our experimental setting is sensitive enough to reveal an attention-hold effect, which would facilitate the interpretation of results from the semantically incongruent condition, particularly in the case of a null result in the latter.

There were four possible outcomes of the experiment with respect to the main hypothesis:

- (1) both disgust-evoking and incongruent scenes hold attention for longer (in comparison to control conditions of happy and congruent scenes): this would replicate and generalize the results of van Hooff et al. (2013, 2014) and reveal that the same effect is caused by incongruent scenes.
- (2) disgust-evoking scenes hold attention, but incongruent scenes do not: this would replicate and generalize the results of van Hooff et al. (2013, 2014) and demonstrate that the procedure is sensitive, which would allow the conclusion that incongruent scenes do not cause the same effect.

- (3) disgust-evoking scenes do not hold attention, but incongruent scenes do: this would demonstrate that the procedure is, in principle, sensitive, and that incongruent scenes hold attention; however, it would indicate that the results of van Hooff et al. (2013, 2014) do not generalize or replicate.
- (4) neither disgust-evoking nor incongruent scenes hold attention: this outcome would suggest that incongruent scenes do hold attention and that the results of van Hoff et al. (2013, 2014) do not generalize or replicate. Importantly this outcome does not allow any conclusions about the sensitivity of the procedure, thus any interpretations should be treated with caution.

2. Method

2.1. Participants and sample-size estimation

For the present study, 46 healthy individuals (3 left-handed; age: M = 26.4, SD = 4.5, range = 18–35 years) were recruited via social media. The sample was gender balanced (23 females). Exclusion criteria were any diagnosed neurological or neuropsychiatric disorders, and deviating from normal, uncorrected vision. Participants signed an informed consent form and were financially compensated for their time. All experimental procedures were approved by the Research Ethics Committee at Nicolaus Copernicus University (KB 447/2020).

The sample size necessary for the planned $2 \times 2 \times 3$ repeated-measures ANOVA analysis (see the Planned Analyses section) was estimated using a simulation-based power analysis conducted with the ANOVA_exact Shiny app (Lakens and Caldwell, 2021; https://arcstats.io/shiny/anova-exact/). In the simulations, we used the mean reaction times (RT) reported by van Hooff et al. (2014), who observed mean RT equal to 534 ms, 522 ms, and 500 ms in the disgust-evoking condition (for 100, 200 and 300 ms SOAs, respectively), and 518 ms, 502 ms, and 490 ms in the happiness-evoking control condition. Common standard deviation was set to 60 ms in the simulation, a value that was calculated based on the SEM displayed in Fig. 3 in van Hoff et al. (2014). The correlation between factors was estimated on the basis of our previous RT data (Furtak et al., 2020) and was set to 0.8.

Using these parameters, we conducted simulations of two extreme scenarios. In the first one, we assumed that incongruent scenes compared to congruent ones would evoke an identical RT effect as disgust-evoking images compared to happiness-evoking ones. In the second one, we assumed that incongruent scenes would not evoke any RT effect at all (mean RT for incongruent scenes would be the same as for congruent and happiness-evoking scenes). In both simulations the alpha value was set to 0.05, and the desired power level was set to 0.9. The first simulation indicated that 14 participants would be enough to achieve the desired level of statistical power for the main effect of interest (*saliency*, see the Operationalization section); in the second simulation, a sample size of 46 participants resulted in the desired power of both the *saliency* effect and the *saliency* × *stimulus type* interaction.

We thus stopped collecting data once 46 valid datasets had been acquired. No data analysis was conducted prior to collecting all the datasets, except for checking the exclusion criteria described in section 6.

2.2. Apparatus

Stimuli were displayed on a DELL AW2518HF LCD monitor (24.5") with 1920*1080 resolution and 120 Hz refresh rate. The experimental procedure was programmed and presented using Presentation® software (Version 20.1, Neurobehavioral Systems, Inc., Berkeley, CA). Participants were seated in a dimly lit, sound-attenuated room. The viewing distance of 60 cm was maintained by an adjustable chinrest.

2.3. Stimuli

Two sets of stimuli were used. The first was a subset of 50 pairs of scenes from the set developed by Mudrik et al. (2010) and recently validated by Shir et al. (2021). In each pair, the congruent version of a scene presents a person performing an action with an object that is highly probable in a given context (e.g., a man playing a violin), whereas in the incongruent version the key object has a very low probability of occurring in the given context (e.g., a man "playing" a broomstick). In both versions, the critical object was pasted onto the scene to avoid any confounds that could result from pasting an object in the incongruent version only. Low-level image properties, like contrast and luminance, were digitally equalized within each stimuli pair. The stimulus set has been validated and used in several previous studies (e.g., Mudrik et al. 2011, 2014; Moors et al., 2016; Mack et al., 2017; Biderman and Mudrik 2018; Faivre et al. 2019; Furtak et al., 2020).

The study of van Hooff et al. (2014) demonstrated that disgust-evoking images hold attention, but neutral, happy and sad images do not. However, an important limitation of the study of van Hooff and colleagues is that they selected and used only 10 images per emotional category from the International Affective Picture System (IAPS) stimulus set (Lang et al., 2008). Using only 10 images per category might have been the reason for the observed rapid habituation effect. Therefore, in the present study we aimed to replicate and generalize their findings by using 50 disgust-evoking and 50 happiness-evoking images. Images were selected from the Nencki Affective Picture System (NAPS), which is a set of modern, high-quality images that are suitable for use in different cultures (Marchewka et al., 2014). Happy images were used as a control condition as, in comparison to neutral images, they are better matched to disgust-evoking images in terms of content and arousal. Selection of images was based on their characteristics in terms of the discrete emotional categories provided by Riegel et al. (2016) and was conducted in the following way: first, we aimed to achieve maximal homogeneity of emotion categories within each subset (by selecting images that were assigned to one emotion category only); second, we aimed to maintain diversity of the presented content within the disgust- and happiness-evoking subsets (i.e., people, faces, animals,

objects, landscapes) while keeping the number of images representing each content type equal between subsets. Thus, the chosen disgust-evoking images depict unpleasant or disturbing scenes that convey negative emotional content (e.g., cockroach, spoiled food, mutilated bodies), while happiness-evoking images present cheerful, positively loaded scenes (e.g., puppy, appetizing food, people playing sports)¹. During the selection process, we intended to keep the means of the arousal scores in both stimuli conditions as close as possible, but disgust-evoking stimuli were in general more arousing (Fig. 1, $M_{\text{disgust}} = 6.26$; $M_{\text{happy}} = 4.46$; t(98) = 13.15; p < 0.001). We confirmed that the disgust-evoking and happy subsets did not differ in terms of low-level properties like luminance, contrast, and entropy.

It is noteworthy that images from the congruent/incongruent subset have a vertical orientation, while NAPS images have a horizontal orientation, but they all maintain the same proportion between the long and the short edges. Therefore, they could be presented in a way that equalizes the area covered on the screen without any image distortions. Importantly, low-level properties (e.g., luminance and contrast) were not equalized between sets as this would have changed the properties of the stimuli and prevented comparisons of our results with results of previous studies using these images. Because the properties of the stimuli were not matched between sets, stimuli from both sets were presented in separate blocks (as described in the Procedure section).

2.4. Procedure

The experimental procedure used in the present study was developed by van Hoff et al. (2013, 2014). In our study, the procedure comprised 1,200 trials in total and lasted approximately 1 h 10 min. A short break was provided after each 75 trials, and its duration was controlled by the participant. Trials were arranged in 8 blocks, each of 150 trials. Congruent/incongruent stimuli were presented in half of the blocks; in the other half, the pictures came from the NAPS set. Blocks comprising congruent/incongruent and disgust-evoking/happy images were presented alternately, with the first block type counterbalanced across participants. Within blocks, each stimulus category (i.e., congruent vs. incongruent scene, or disgust- vs happiness-evoking) appeared in an equal number of trials. Furthermore, for each stimulus category, the target letter was presented with one of three stimulus onset asynchronies (SOA) with respect to the scene image (100 ms, 200 ms, 300 ms), and each SOA occurred in $\frac{1}{3}$ of trials. Therefore, there were 100 trials per each image category and the SOA condition. The order of trials of different conditions was randomized within blocks.

All stimuli were presented against a gray background (RGB [128, 128, 128]; Fig. 2). Each trial began with a white fixation cross ($0.85^{\circ} \times 0.85^{\circ}$ of visual angle) displayed in the center of the screen for a random duration between 1500 and 2500 ms. The fixation cross was followed by a scene ($4.10^{\circ} \times 6.87^{\circ}$ for congruent/incongruent images, and $6.87^{\circ} \times 4.10^{\circ}$ for disgust-evoking/happy images) presented centrally and remaining on the screen for 1200 ms or until the participant's response to the target letter. A white target letter 'N' or 'Z' (Arial, 15pt, $0.37^{\circ} \times 0.37^{\circ}$) was displayed 100 ms, 200 ms, or 300 ms after the scene onset in one of four peripheral locations (on the left, on the right, above or below the scene), 5.04° from the center of the screen. The target letter was presented for 50 ms.

The participants' task was to identify the peripheral letters 'N' or 'Z' and respond accordingly with a button press as quickly and accurately as possible. Letters and their locations were pseudorandomized across trials (with the control for the frequency of each letter/location condition for each stimulus category and display time condition). The trial ended after either a valid response (after the letter onset), or 5000 ms after the letter onset if there was no response. Participants responded by pressing one of two response buttons (using their left and right index fingers). The location of the response buttons in relation to the target letters was counterbalanced across participants (i.e., half of participants responded with the left button to "N" and the right button to "Z", while the other half responded with the left button to "Z" and the right button to "N").

In relation to van Hooff et al.'s (2013, 2014) studies, our procedure was characterized by the following changes. First, we included only the short SOAs (100, 200, 300 ms) that were used by van Hooff and colleagues, but we did not include the longer ones (500, 800 ms). Second, we increased the number of trials per condition (from 40 to 100) in order to increase the precision of within-subjects estimates. Third, the duration of the fixation cross was randomly selected in order to minimize the influence of learned reflexive behavior on the effect of interest.

2.5. Operationalization

<u>Independent variables</u>: The following three variables were included in the analysis as factors: *stimulus type* (semantic vs affective stimuli); *stimulus saliency* (salient, potentially attention-holding stimuli [semantically incongruent or disgust-evoking images] vs.

¹ NAPS ids of disgust-evoking pictures: Animals_018_h, Animals_027_h, Animals_032_h, Animals_033_h, Animals_037_h, Animals_041_h, Animals_043_h, Animals_047_h, Animals_062_h, Animals_065_h, Animals_078_h, Animals_221_h, Faces_156_h, Faces_264_h, Faces_266_h, Faces_366_h, Landscapes_007_h, Objects_006_h, Objects_017_h, Objects_010_h, Objects_011_h, Objects_013_h, Objects_019_h, Objects_022_h, Objects_053_h, Objects_060_h, Objects_109_h, Objects_122_h, Objects_125_h, Objects_126_h, Objects_154_h, Objects_206_h, Feople_057_h, Feople_058_h, People_087_h, People_233_h, People_202_h, People_202_h, People_216_h, People_217_h, People_220_h, People_223_h, People_223_h, People_228_h, People_233_h, People_239_h, People_240_h, People_241_h. Happiness evoking pictures: Animals_100_h, Animals_117_h, Animals_122_h, Animals_131_h, Animals_158_h, Animals_177_h, Animals_183_h, Animals_184_h, Animals_186_h, Animals_187_h, Animals_220_h, Objects_086_h, Objects_086_h, Objects_099_h, Objects_077_h, Objects_078_h, Objects_086_h, Objects_192_h, Objects_201_h, People_235_h, Objects_078_h, Objects_086_h, Objects_192_h, Objects_201_h, People_044_h, People_055_h, People_056_h, Objects_276_h, Objects_078_h, Objects_086_h, Objects_192_h, People_026_h, People_044_h, People_055_h, People_067_h, People_068_h, People_066_h, People_103_h, People_116_h, People_07_h, People_07_h, People_185_h, People_055_h, People_067_h, People_066_h, People_103_h, People_116_h, People_176_h, People_176_h, People_180_h, People_185_h, People_185_h, People_185_h, People_185_h, People_106_h, People_103_h, People_106_h, People_106_h, People_106_h, People_185_h, People_190_h, People_192_h.



Fig. 1. Scatter plot demonstrating arousal and valence ratings of the disgust- and happiness-evoking NAPS images chosen for the present study (Riegel et al., 2016).

control stimuli [semantically congruent or happiness-evoking images]); and SOA (short [100 ms], medium [200 ms], long [300 ms]). All independent variables were introduced in a within-subject design.

<u>Dependent variables:</u> Reaction times (RT) of correct responses to the target letters were defined as a primary measure. We aggregated RT data for each condition by calculating the median, which is the most appropriate statistic to describe variables that deviate from the normal distribution. Accuracy of responses to the target letters, defined as the proportion between correct responses and all valid responses (correct or incorrect), served as a secondary measure.

<u>Hypothesis:</u> We expected salient stimuli (semantically incongruent or disgust-evoking images) to cause an attention-hold effect which would be reflected by longer RTs and lower accuracy of responses to target letters when compared to control stimuli (semantically congruent or happiness-evoking).

2.6. Exclusion criteria

<u>Participants</u>: A participant was excluded if he/she failed to complete the experimental procedure or exhibited a letter discrimination accuracy lower than 70% in any of the stimulus category/SOA conditions.

<u>Trials</u>: For the RT analysis, we excluded trials with no response or an incorrect response, and correct trials in which reaction times were shorter than 200 ms or longer than 1600 ms with respect to the target letter onset. For the accuracy analysis, we excluded no-response trials and trials in which reaction times were shorter than 200 ms or longer than 1600 ms with respect to target letter onset.

2.7. Planned analyses

All statistical analyses were conducted using the SciPy package (Virtanen et al., 2020) and JASP 0.9.0.1 software (JASP Team, 2018) and cross-checked with the Statcheck web app (Rife et al., 2016, https://statcheck.io).

We conducted confirmatory analyses of the RT and accuracy effects related to the following factors: *stimulus type* (2 levels), *stimulus saliency* (2 levels), and *SOA* (3 levels). Therefore, we used a $2 \times 2 \times 3$ repeated-measures ANOVA. Our main focus was on the influence of *stimulus saliency* on RT and accuracy in the letter-classification task as this made it possible to verify whether semantically incongruent or disgust-evoking stimuli held attention. The following interactions of *stimulus saliency* with other variables were also examined:

- (1) The interaction of *stimulus saliency* with *stimulus type* factor and follow-up simple main effects; this allowed verification of our hypothesis concerning the attention-holding properties of semantically incongruent and disgust-evoking scenes (in comparison to control stimuli) and revealed potential differences between these two stimulus types.
- (2) The interaction of *stimulus saliency* and *SOA*, which demonstrated the time course of the attention-hold effect.

A) TRIAL SCHEME

response window (<5000 ms)



Fig. 2. Schematic presentation of a trial sequence (A) and representative stimuli used in the four conditions of the experiment (B).

3. Data and materials

All data (raw and aggregated) and materials (scripts used to present the procedure and analyze data) used in the study are freely available from the Open Science Framework (OSF; <u>https://osf.io/7a8jt/</u>).

4. Results

Participants' performance in the designed procedure was very accurate, thus the percentage of trials that were valid and entered the analysis was high (Mdn = 99.6%, range = [92.4%, 100%]). All participants discriminated target letters with accuracy higher than 70% in all of the conditions (pooled accuracy from all conditions: Mdn = 95.1%, range = [86.6%, 98.7%]). Therefore, none of the recruited participants were excluded from the sample.

A)



Fig. 3. Reaction times (A) and response accuracy scores (B) 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).

4.1. Primary measure: Reaction times

Median RT values were analyzed using a three-way repeated-measures ANOVA, with *stimulus type, stimulus saliency*, and *SOA* as factors (Fig. 3). The *stimulus saliency* factor is crucial for the conducted analysis, as it reflects attention hold properties of semantically incongruent and disgust-evoking stimuli, and therefore only effects and interactions comprising this factor are reported. Results were interpreted according to the highest-order significant interaction (Meyers et al., 2006) and followed up by the analysis of simple effects (Howell, 2009) or post-hoc tests necessary to fully understand the outcome. RT values observed at different levels of *SOA* violated the sphericity assumption, thus all effects that involved *SOA* were corrected using the Greenhouse-Geisser correction. The analysis revealed a significant three-way interaction between *stimulus type, stimulus saliency*, and *SOA* (F(1.94, 87.45) = 9.05, p < 0.001, $\eta_p^2 = 0.17$). Such an interaction means that the attention-hold effect, as indicated by RT, depends differently on *SOA* in both stimuli sets (semantic and affective). We also found a significant 2-way interaction between *stimulus saliency* and *stimulus type* (F(1, 45) = 28.10, p < 0.001, $\eta_p^2 = 0.38$) and a significant main effect of *stimulus saliency* (F(1, 45) = 38.51, p < 0.001, $\eta_p^2 = 0.46$). The two-way interaction between *stimulus saliency* and *SOA* did not reach the significance level (F(1.91, 85.88) = 1.88, p = 0.159). Therefore, further analysis steps were performed to explore and interpret the highest-level, three-way interaction. These specific analyses were not part of the registration document, but they are in the spirit of analyzing the details of the three-way interaction.

To examine simple interactions and main effects that can reveal the exact relations between the three factors (*stimulus type*, *stimulus saliency*, and *SOA*), a two-way repeated-measures ANOVA with *stimulus saliency* and *SOA* was conducted separately for each level of *stimulus type* (semantic and affective stimuli). In the semantic condition we obtained a non-significant two-way interaction between *stimulus saliency* and *SOA* (F(2, 90) = 1.25, p = 0.291), and a non-significant main effect of *stimulus saliency* (F(1, 45) = 2.00, p = 0.165). Therefore, we conclude that the RT attention-hold effect was not caused by incongruent stimuli in any of the *SOA* conditions.

The same analysis performed on affective stimuli revealed a significant two-way interaction between *stimulus saliency* and *SOA* (*F*(2, 90) = 11.31, p < 0.001, $\eta_p^2 = 0.20$), which suggests that *SOA* affected RT differently for the presentation of disgust-evoking images than for happiness-evoking ones. Follow-up analysis of the simple main effects provided evidence for a significant *stimulus saliency* effect in all *SOA* conditions (100 ms: *F*(1, 45) = 38.46, p < 0.001; 200 ms: *F*(1, 45) = 42.41, p < 0.001; 300 ms: *F*(1, 45) = 10.75, p = 0.002) meaning that the attention-hold effect was present in all *SOA* conditions. Finally, we conducted 3 contrasts with Holm corrections for multiple comparisons on the differences in RT effects induced by disgust- evoking stimuli between 3 *SOA* levels. These tests revealed that the RT effects in the 100 ms and 200 ms SOA conditions did not differ from each other (t(45) = 0.18, $p_{holm} = 0.859$), but both were higher than the effect for the 300 ms SOA condition (100 ms vs 300 ms: t(45) = 4.20, $p_{holm} < 0.001$, d = 0.62; 200 ms vs 300 ms: t(45) = 4.03, $p_{holm} < 0.001$, d = 0.59). Thus, we conclude that the attention-hold effect for disgust-evoking images was stronger for short SOAs in comparison to the 300 ms SOA.

4.2. Secondary measure: Response accuracy

A similar three-way repeated measures ANOVA was conducted on response accuracy scores (Fig. 3). We obtained a significant twoway interaction between *stimulus saliency* and *stimulus type* (F(1, 45) = 10.61, p = 0.002, $\eta^2_p = 0.19$), which means that the relation between accuracy scores for salient vs control stimuli differed between semantic and affective sets of images. Neither of the other effects concerning the *stimulus saliency* factor was significant (*stimulus saliency*: F(1, 45) = 1.16, p = 0.288; *stimulus saliency* × *SOA*: F(2,90) = 0.03, p = 0.971; *stimulus saliency* × *stimulus type* × *SOA*: F(2, 90) = 2.22, p = 0.115). Analysis of simple main effects of *stimulus saliency* on different levels of *stimulus type* revealed that a significant attention-hold effect was present for disgust-evoking (F(1, 45) = 12.38, p = 0.001) but not for semantically incongruent scenes (F(1, 45) = 0.73, p = 0.40). Therefore, results of the accuracy scores analysis are in line with results of the RT analysis.

4.3. Unplanned analyses

Bayesian repeated measures ANOVA and targeted Bayesian comparisons were conducted to provide further support for the null result obtained in the planned frequentist analysis in the semantic condition. Bayesian ANOVA analysis was performed with Cauchy priors (r = 0.5) for a fixed effect, while for Bayesian t-tests Cauchy priors (r = 0.707) were used. Bayes factors were interpreted according to the guidelines proposed by Wetzels et al. (2011).

The Bayesian ANOVA indicated that the observed RT data are most likely under the model comprising *stimulus saliency, stimulus type, SOA,* and a 2-way interaction between *stimulus saliency* and *stimulus type* (P(M) = 0.053; P(M|data) = 0.845; $BF_{10} = 0.023$ for a full model and $BF_{10} < 1e-5$ for a model comprising only main effects, compared to the best model). Thus, we concluded that the effect of saliency differs between affective and semantic stimuli. The analysis of the prediction power of effects across all matched models revealed extreme evidence in favor of inclusion of *stimulus saliency* × *stimulus type* interaction ($BF_{incl} > 1e + 5$), strong evidence against the inclusion of *stimulus saliency* × *stimulus saliency* × *stimulus type* interaction ($BF_{incl} = 3.903$). Therefore, although the best model does not account for the 3-way interaction, there is evidence that this interaction occurs in the data.

Furthermore, we conducted 6 Bayesian paired-sample t-tests to compare the RT effect for each combination of *stimulus set* and *SOA*. For semantic stimuli Bayes factors indicated that there is substantial evidence against the difference between salient and control stimuli for 100 ms SOA ($BF_{10} = 0.131$) and 200 ms SOA ($BF_{10} = 0.279$), and anecdotal evidence for the effect for 300 ms SOA ($BF_{10} = 2.211$). Bayes factors obtained for affective stimuli implied extreme evidence of a saliency effect for 100 ms SOA ($BF_{10} > 1e + 5$) as well as for 200 ms SOA ($BF_{10} > 1e + 5$), and very strong evidence for 300 ms SOA ($BF_{10} = 31.330$). Thus, Bayesian analysis provided further support for the conclusions that attention is held by disgust-evoking but not by semantically incongruent stimuli.

An analogous analysis was conducted for accuracy scores. The observed accuracy scores are most likely under the model comprising *stimulus saliency, stimulus type*, and a 2-way interaction between these two factors (P(M) = 0.053; P(M|data) = 0.574; $BF_{10} = 0.004$ for a full model and $BF_{10} = 0.024$ for a model comprising main effects of *stimulus saliency* and *stimulus type*, compared to the best model). Further, we found very strong evidence for inclusion of a *stimulus saliency* × *stimulus type* interaction ($BF_{incl} = 42.628$), strong evidence against the inclusion of *stimulus saliency* × *SOA* interaction ($BF_{incl} = 0.040$), and anecdotal evidence against a 3-way interaction of *stimulus saliency, stimulus type* and *SOA* ($BF_{incl} = 0.392$). Pairwise comparisons between salient and control stimuli from the semantic set revealed strong evidence against the effect for 100 ms SOA ($BF_{10} = 0.058$) and substantial evidence against the effect for 200 ms SOA ($BF_{10} = 0.109$) as well as for 300 ms SOA ($BF_{10} = 0.232$). Evidence for an attention hold effect elicited by affective stimuli was very strong for 100 ms SOA ($BF_{10} = 74.124$) and substantial for 200 ms SOA ($BF_{10} = 3.041$). But for 300 ms SOA we found anecdotal evidence against the effect ($BF_{10} = 0.692$). In summary, Bayesian analysis of accuracy scores confirmed that semantically incongruent stimuli do not hold attention, while disgust-evoking stimuli elicit a robust attention hold effect.

5. Discussion

Mechanisms of selective attention are typically investigated with stimuli defined by simple physical features and presented in arrays of mutually independent items. Such basic studies provide crucial insights into the mechanisms of attention, but how their findings translate into more naturalistic settings is not well understood. While naturalistic environments are inherently more complex and crowded, they are also characterized by spatial and semantic regularities that, by introducing expectations regarding the location and identity of objects, might effectively facilitate attentional selection (Peelen and Kastner, 2014; Wu et al., 2014; Kaiser et al., 2019; Wolfe and Horowitz, 2017; Võ et al., 2019).

The present study was therefore designed to investigate how the semantic relations present in real-world scenes affect the functioning of spatial attention. Importantly, while the majority of previous studies focused on identifying features that *attract* attention in scenes, here we investigated attention engagement, which is a different and relatively under-researched mechanism. Specifically, we tested whether spatial attention is automatically engaged and held by violations in the semantic composition of real-world scenes. However, we found no such effect: objects that were semantically incongruent did not hold attention for longer than congruent ones. Conducted Bayesian analysis confirmed that collected data support lack of effect in the semantically incongruent condition. What proves that our procedure was, in principle, effective and sensitive – and thus further strengthens the interpretation of the observed null result – is the results from the "positive control" condition, in which both the reaction times and accuracy scores indicate that the disgust-evoking scenes did hold attention (in line with van Hooff et al., 2013, 2014). Below we discuss both the null effect in the semantic condition and the attention-hold effect in the affective condition in light of previous research.

5.1. Semantically incongruent scenes do not hold spatial attention

Comparing the perception of semantically congruent and incongruent objects is one of the most informative ways of investigating the role of contextual relations in natural scenes (Biederman et al., 1982). It is now well established that objects that are semantically incongruent and do not benefit from contextual facilitation (Bar, 2004) are recognized more slowly and less accurately in comparison to congruent ones (Boyce et al., 1989; Davenport and Potter, 2004; Davenport, 2007; Joubert et al., 2008; Fize et al., 2011; Mack et al., 2017; Leroy et al., 2020; Furtak et al., 2022). Furthermore, perception of incongruent objects is associated with greater amplitude of ERP components (Mudrik et al., 2010; Vo and Wolfe, 2013; Truman and Mudrik, 2018) and stronger activity of several brain regions, including visual and cognitive-system areas, as assessed with fMRI (Rémy et al., 2014; Faivre et al., 2019). The results of these neuroimaging studies are taken as evidence that greater involvement of neural and cognitive resources is necessary in order to resolve the semantic conflict and eventual recognition of incongruent objects. Accordingly, it has been proposed that incongruent objects preferentially engage attention and hold it for longer. Several eye-tracking studies have indeed found that once participants fixated on a semantically incongruent object, they maintained their gaze for longer in comparison to a congruent object (Henderson et al., 1999; Underwood et al., 2008; Vo and Henderson 2009, 2011; Cornelissen and Vo, 2017). However, our data tell a different story and challenge the conclusions of these previous studies: by using an experimental paradigm designed to measure an automatic hold of covert spatial attention and analyzing both reaction times and accuracy scores, we found no evidence that semantically incongruent objects hold attention for longer than semantically congruent ones. Conducted Bayesian analysis revealed that our data provide strong evidence against such an effect.

When discussing the results of previous eye-tracking studies, it is important to point out that in many of them the presented objects were not completely task-irrelevant (as discussed by Cornelissen and Vo, 2017). Consequently, it is unclear whether the observed gazehold effect was truly automatic. To address this, Cornelissen and Vo (2017) designed a study in which participants were tasked with searching for a target letter overlaid on a centrally presented image of a scene. Even though the scene image was completely taskirrelevant, participants still exhibited prolonged gaze duration when fixating on incongruent objects in comparison to congruent ones. How can this difference in results and conclusions between Cornelissen and Vo's study (2017) and our study be explained? First, by differences in the spatial arrangement of the presented stimuli. In Cornelissen and Vo's paradigm (2017), the scene image was bigger than in our study and provided a reference frame for the main search task. Conversely, in our experiment a relatively smaller scene image was displayed centrally, whereas targets were presented peripherally and did not overlap spatially with the scene. Second, the temporal aspect also differs between both studies. In Cornelissen and Vo's paradigm (2017), participants searched through an array of targets at their own pace, which might have provided them with more time to recognize the structure of the scene and generate expectations regarding the locations and identities of objects (even though the scene was presented in the background). In contrast, in our experiment the targets appeared shortly after the scene's onset (SOA between 100 ms and 300 ms), thus the time available to recognize the scene was limited. However, recognition of both the gist of the scene and the main objects present in it is very rapid and automatic (e.g., Joubert et al., 2007, 2008; Furtak et al., 2022), thus short inspection times are unlikely to affect these processes. Finally, an important difference is that Cornelissen and Vo (2017) investigated markers of overt attention in the form of eye movements. In contrast, our experimental paradigm was designed to capture the covert aspect, as participants were asked to maintain their gaze on the centrally presented fixation cross at all times (and the target presentation time was short in order to prevent eye movements to the target). The overt and covert aspects of attention are typically strongly correlated, but in principle they can be dissociated (e.g., Hunt and Kingstone, 2003), which might potentially contribute to the different patterns of results observed between these studies.

The paradigm used in the present study was designed by van Hoff and colleagues (2013, 2014) to investigate the automatic and covert component of attentional selection. However, one might argue that the features introduced to test automaticity (i.e., short SOAs, task-irrelevance of a scene) might limit the procedure's sensitivity to detect the attention-hold effect. This concern is mitigated, first, by

the fact that the procedure was validated by van Hoff and colleagues (2013, 2014), who across two studies found this paradigm to be suitable for the investigation of attention hold by complex scenes. Second and most importantly, this concern is mitigated by data from the "positive control" condition included in our study, in which we found that the disgust-evoking scenes did hold attention. This strongly indicates that the procedure was, in principle, effective and sensitive enough. However, one could still argue that the effect in the semantic condition exists but is much weaker than in the affective condition. While such an argument cannot be completely refuted, in order to detect even a potentially very subtle effect of incongruence (i.e., much weaker than in the emotional condition) we included more trials per condition and tested a bigger sample of participants in comparison to the original studies by van Hooff and colleagues (2013, 2014). Thus, we were able to obtain better estimates of the within-subject effect with respect to the between-subjects variance. Another potential concern might be that the effect of affective stimuli is indeed rapid and automatic, but more time is required to recognize semantic incongruence. To test for such a possibility, we included the 300 ms SOA condition. In the planned frequentist analysis we did not find a significant effect in the semantically incongruent condition, neither in RT, nor in accuracy scores. The Bayesian analysis of accuracy scores supported the null effect, but analysis of RT provided anecdotal evidence that incongruent scenes do hold attention for longer than the congruent ones. Therefore, future studies might investigate attentional prioritization of incongruence using longer SOAs, which we did not use here in line with our aim to focus on the automatic aspect of attention hold. Overall, our study provides robust evidence that attention is preferentially engaged by disgust-evoking scenes, but no such effect is caused by semantically incongruent scenes.

What further strengthens our conclusion that incongruent objects do not hold attention is that we employed scene images from the most commonly used and well-tested set of stimuli, which was developed by Mudrik and colleagues (2010). All images from this set present a subject performing an action with either a congruent or an incongruent object. Notably, the action-based context creates strong expectations, as typically very few objects are congruent with the presented action. This is confirmed by the results of previous studies which found that incongruent scenes included in the set cause robust effects in behavioral (e.g., Biderman and Mudrik, 2018), ERP (e.g., Mudrik et al., 2010; Truman and Mudrik 2018), and fMRI measures (Faivre et al., 2019), and that participants were able to detect and recognize the incongruence easily (Mudrik et al., 2010; Furtak et al., 2020). Therefore, the null effect we observed cannot be explained by excessively subtle semantic manipulations in the images used. Future studies investigating attention might also test other stimuli sets, for instance those in which congruence is manipulated by presenting natural or artificial objects (animals or furniture) on either natural or artificial (outdoors or indoors) backgrounds (e.g., Rémy et al., 2014; Leroy et al., 2020).

5.2. Disgust-evoking scenes hold spatial attention

While the main goal of our study was to investigate the effect of semantic relations in scenes, the results of the "positive control" condition provide important information regarding the involvement of attention in the perception of emotional content. Specifically, we demonstrate that disgust-evoking images engage and hold attention for longer than happiness-evoking images. This effect was found for all SOAs used in our study, but it was in fact stronger at 100 ms and 200 ms SOAs in comparison to the 300 ms SOA. This indicates that the observed attention hold was rapid and automatic. Therefore, our study closely replicated the results reported by van Hooff and colleagues (2013, 2014).

What can be considered a main limitation of van Hooff and colleagues' (2013, 2014) work is that in their studies only 10 images per emotional category were used (images were selected from the IAPS set; Lang et al., 2008). In contrast, for our study 50 images per emotional category were selected from the NAPS set, which provides a bigger pool of modern and culturally neutral emotional scene images (Marchewka et al., 2014; Riegel et al., 2016). Thus, by revealing the same effect using a bigger subset of images from a different set, we not only replicated van Hooff and colleagues' findings (2013, 2014) but also confirmed their robustness and generalizability.

In the "positive control" condition of our study, the disgust-evoking scenes were compared to happiness-evoking scenes, as the latter were not found to hold attention in previous studies and thus constituted an appropriate baseline (van Hooff et al., 2013, 2014). We did not include other emotional categories, like fearful or neutral images, as investigating the specificity of disgust-related effects was not the main goal of our work. Previous studies suggest that disgust indeed exhibits a specific behavioral and neural signature in comparison to all other basic emotions. More specifically, disgust is associated with a tendency to narrow attention and inspect the disgust-evoking object more closely (Gable & Harmon-Jones, 2010; Carretié et al., 2011). This hypothesis is supported by the attention-hold effect observed in our study, and by studies showing that disgust-evoking stimuli are remembered better in comparison to other emotional categories (Chapman et al., 2013, Croucher et al., 2011; Riegel et al., 2022). Furthermore, ERP studies found that disgust-evoking images evoke a larger frontal P2 ERP component (Carretié et al., 2011) and a larger early posterior negativity (EPN; Wheaton et al., 2013) in comparison to fear-evoking images. Both ERP components occur early, around 200 ms post-stimulus, therefore they could be related to early attentional engagement. Importantly, a potential limitation when interpreting the results of the "positive control" condition is that the disgust-evoking images are typically rated as most arousing, therefore matching them to control stimuli in this dimension is difficult to do.

Finally, the block design can be considered as another limitation of our work: the affective (disgust-evoking/happy) and semantic (congruent/incongruent) images were presented in two separate blocks, the order of which was counterbalanced between participants. While presenting all images in random order might potentially strengthen the investigated effects, the block design was used because both sets differed in terms of low-level properties (luminance, contrast). These properties were not normalized between sets, as changing them would have made comparison to other studies using the same stimuli problematic and would prevent referring to the subjective evaluations collected for NAPS images in validation studies (Marchewka et al., 2014; Riegel et al., 2016).

6. Conclusions

In conclusion, our recently published study revealed that semantically incongruent objects do not capture attention automatically (Furtak et al., 2020), while the present study provides evidence that such objects do not hold attention either. Therefore, by showing that violation of semantic relations is not preferentially selected by spatial attention, our work imposes important constraints on existing and future theoretical models that describe how attention operates in complex naturalistic settings.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Bar, M. (2004). Visual objects in context. Nature Reviews Neuroscience, 5(8), 617-629.

- Becker, M. W., Pashler, H., & Lubin, J. (2007). Object-intrinsic oddities draw early saccades. Journal of Experimental Psychology: Human Perception and Performance, 33 (1), 20.
- Biderman, N., & Mudrik, L. (2018). Evidence for implicit-but not unconscious-processing of object-scene relations. Psychological Science, 29(2), 266-277.
- Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene perception: Detecting and judging objects undergoing relational violations. Cognitive Psychology, 14 (2), 143–177.
- Bindemann, M., Burton, A. M., Hooge, I. T., Jenkins, R., & De Haan, E. H. (2005). Faces retain attention. Psychonomic Bulletin & Review, 12(6), 1048–1053.
- Furtak, M., Mudrik, L., & Bola, M. (2022). The forest, the trees, or both? Hierarchy and interactions between gist and object processing during perception of real-world scenes. Cognition, 221, Article 104983.
- Bonitz, V. S., & Gordon, R. D. (2008). Attention to smoking-related and incongruous objects during scene viewing. Acta psychologica, 129(2), 255-263.
- Boyce, S. J., Pollatsek, A., & Rayner, K. (1989). Effect of background information on object identification. Journal of Experimental Psychology: Human Perception and Performance, 15(3), 556.
- Carretié, L., Ruiz-Padial, E., López-Martín, S., & Albert, J. (2011). Decomposing unpleasantness: Differential exogenous attention to disgusting and fearful stimuli. *Biological Psychology*, 86(3), 247–253.
- Chapman, H. A., Johannes, K., Poppenk, J. L., Moscovitch, M., & Anderson, A. K. (2013). Evidence for the differential salience of disgust and fear in episodic memory. Journal of Experimental Psychology: General, 142(4), 1100.
- Cornelissen, T. H., & Vô, M. L. H. (2017). Stuck on semantics: Processing of irrelevant object-scene inconsistencies modulates ongoing gaze behavior. Attention, Perception, & Psychophysics, 79(1), 154–168.
- Croucher, C. J., Calder, A. J., Ramponi, C., Barnard, P. J., & Murphy, F. C. (2011). Disgust enhances the recollection of negative emotional images. *PloS one, 6*(11), Article e26571.
- Davenport, J., L. (2007). Consistency effects between objects in scenes. Memory & Cognition, 35(3), 393-401.
- Davenport, J. L., & Potter, M. C. (2004). Scene consistency in object and background perception. Psychological Science, 15(8), 559–564.
- De Graef, P., Christiaens, D., & d'Ydewalle, G. (1990). Perceptual effects of scene context on object identification. Psychological Research, 52(4), 317–329.
- Faivre, N., Dubois, J., Schwartz, N., & Mudrik, L. (2019). Imaging object-scene relations processing in visible and invisible natural scenes. Scientific Reports, 9(1), 1–13.
 Fize, D., Cauchoix, M., & Fabre-Thorpe, M. (2011). Humans and monkeys share visual representations. Proceedings of the National Academy of Sciences, 108(18), 7635–7640.
- Folk, C. L., Ester, E. F., & Troemel, K. (2009). How to keep attention from straying: Get engaged! Psychonomic Bulletin & Review, 16(1), 127-132.
- Furtak, M., Doradzińska, Ł., Ptashynska, A., Mudrik, L., Nowicka, A., & Bola, M. (2020). Automatic attention capture by threatening, but not by semantically incongruent natural scene images. Cerebral Cortex, 30(7), 4158–4168.
- Gable, P., & Harmon-Jones, E. (2010). The blues broaden, but the nasty narrows: Attentional consequences of negative affects low and high in motivational intensity. *Psychological Science*, *21*(2), 211–215.
- Gareze, L., & Findlay, J. M. (2007). Absence of scene context effects in object detection and eye gaze capture. In Eye Movements (pp. 617-637). Elsevier.
- Henderson, J. M., & Hollingworth, A. (1999). High-level scene perception. Annual Review of Psychology, 50(1), 243–271.
- Henderson, J. M., Weeks, P. A., Jr, & Hollingworth, A. (1999). The effects of semantic consistency on eye movements during complex scene viewing. Journal of Experimental Psychology: Human Perception and Performance, 25(1), 210.
- Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. Neuron, 36(5), 791-804.
- Hollingworth, A., & Henderson, J. M. (2000). Semantic informativeness mediates the detection of changes in natural scenes. *Visual Cognition*, 7(1–3), 213–235.
- Howell, D. C. (2009). Statistical methods for psychology, Toronto. ON: Nelson Education.
- Hunt, A. R., & Kingstone, A. (2003). Inhibition of return: Dissociating attentional and oculomotor components. Journal of Experimental Psychology: Human Perception and Performance, 29(5), 1068.
- Joubert, O. R., Fize, D., Rousselet, G. A., & Fabre-Thorpe, M. (2008). Early interference of context congruence on object processing in rapid visual categorization of natural scenes. Journal of Vision, 8(13).
- Joubert, O. R., Rousselet, G. A., Fize, D., & Fabre-Thorpe, M. (2007). Processing scene context: Fast categorization and object interference. Vision Research, 47(26), 3286–3297.
- Juan, C. H., Shorter-Jacobi, S. M., & Schall, J. D. (2004). Dissociation of spatial attention and saccade preparation. Proceedings of the National Academy of Sciences, 101 (43), 15541–15544.
- Kaiser, D., Quek, G. L., Cichy, R. M., & Peelen, M. V. (2019). Object vision in a structured world. Trends in Cognitive Sciences, 23(8), 672-685.
- Kappenman, E. S., Farrens, J. L., Luck, S. J., & Proudfit, G. H. (2014). Behavioral and ERP measures of attentional bias to threat in the dot-probe task: Poor reliability and lack of correlation with anxiety. *Frontiers in Psychology*, *5*, 1368.
- Kappenman, E. S., MacNamara, A., & Proudfit, G. H. (2015). Electrocortical evidence for rapid allocation of attention to threat in the dot-probe task. Social Cognitive and Affective Neuroscience, 10(4), 577–583.

JASP Team (2018). JASP (Version 0.9.0.1)[Computer software].

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

LaPointe, M. R., & Milliken, B. (2017). Conflicting effects of context in change detection and visual search: A dual process account. Canadian Journal of Experimental Psychology/Revue canadianne de psychologie expérimentale, 71(1), 40.

Lakens, D., & Caldwell, A., R. (2021). Simulation-based power analysis for factorial analysis of variance designs. Advances in Methods and Practices in Psychological Science, 4(1), 1–14.

LaPointe, M. R., Lupianez, J., & Milliken, B. (2013). Context congruency effects in change detection: Opposing effects on detection and identification. Visual Cognition, 21(1), 99–122.

Leroy, A., Faure, S., & Spotorno, S. (2020). Reciprocal semantic predictions drive categorization of scene contexts and objects even when they are separate. Scientific Reports, 10(1), 1–12.

Loftus, G. R., & Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. Journal of Experimental Psychology: Human perception and performance, 4(4), 565.

Mack, A., Clarke, J., Erol, M., & Bert, J. (2017). Scene incongruity and attention. Consciousness and cognition, 48, 87-103.

Marchewka, A., Zurawski, Ł., Jednoróg, K., & Grabowska, A. (2014). The Nencki Affective Picture System (NAPS): Introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior Research Methods*, 46(2), 596–610.

Meyers, L. S., Gamst, G., & Guarino, A. J. (2006). Applied Multivariate Research: Design and Interpretation. London: Sage.

Moors, P., Boelens, D., Van Overwalle, J., & Wagemans, J. (2016). Scene integration without awareness: No conclusive evidence for processing scene congruency during continuous flash suppression. *Psychological Science*, 27(7), 945–956.

Morey, R. D. (2008). Confidence intervals from normalized data: A correction to Cousineau (2005). Tutorials in Quantitative Methods for Psychology, 4(2), 61-64.

Mudrik, L., Deouell, L. Y., & Lamy, D. (2011). Scene congruency biases binocular rivalry. Consciousness and Cognition, 20(3), 756-767.

Mudrik, L., Lamy, D., & Deouell, L. Y. (2010). ERP evidence for context congruity effects during simultaneous object-scene processing. *Neuropsychologia*, 48(2), 507–517.

Mudrik, L., Shalgi, S., Lamy, D., & Deouell, L. Y. (2014). Synchronous contextual irregularities affect early scene processing: Replication and extension. *Neuropsychologia*, 56, 447–458.

Oliva, A., & Torralba, A. (2006). Building the gist of a scene: The role of global image features in recognition. Progress in Brain Research, 155, 23–36.

Ortiz-Tudela, J., Martín-Arévalo, E., Chica, A. B., & Lupiáñez, J. (2018). Semantic incongruity attracts attention at a pre-conscious level: evidence from a TMS study. cortex. 102, 96–106.

Ortiz-Tudela, J., Milliken, B., Botta, F., LaPointe, M., & Lupiañez, J. (2017). A cow on the prairie vs. a cow on the street: Long-term consequences of semantic conflict on episodic encoding. *Psychological Research*, 81(6), 1264–1275.

Peelen, M. V., & Kastner, S. (2014). Attention in the real world: Toward understanding its neural basis. Trends in Cognitive Sciences, 18(5), 242-250.

Posner, M. I., Inhoff, A. W., Friedrich, F. J., & Cohen, A. (1987). Isolating attentional systems: A cognitive-anatomical analysis. Psychobiology, 15(2), 107-121.

Rayner, K., Castelhano, M. S., & Yang, J. (2009). Eye movements when looking at unusual/weird scenes: Are there cultural differences? Journal of Experimental Psychology: Learning, Memory, and Cognition, 35(1), 254.

Rémy, F., Vayssière, N., Pins, D., Boucart, M., & Fabre-Thorpe, M. (2014). Incongruent object/context relationships in visual scenes: Where are they processed in the brain? Brain and Cognition, 84(1), 34–43.

Riegel, M., Wierzba, M., Wypych, M., Ritchey, M., Jednoróg, K., Grabowska, A., & Marchewka, A. (2022). Distinct medial-temporal lobe mechanisms of encoding and amygdala-mediated memory reinstatement for disgust and fear. *Neuroimage*.

Riegel, M., Żurawski, Ł., Wierzba, M., Moslehi, A., Klocek, Ł., Horvat, M., ... Marchewka, A. (2016). Characterization of the Nencki Affective Picture System by discrete emotional categories (NAPS BE). Behavior Research Methods, 48(2), 600–612.

Rieger, J. W., Köchy, N., Schalk, F., Grüschow, M., & Heinze, H. J. (2008). Speed limits: Orientation and semantic context interactions constrain natural scene discrimination dynamics. Journal of Experimental Psychology: Human Perception and Performance, 34(1), 56.

Rife, S. C., Nuijten, M. B., & Epskamp, S. (2016). Statcheck: Extract statistics from articles and recompute p-values [web application]. Retrieved from.

Shir, Y., Abudarham, N., & Mudrik, L. (2021). You won't believe what this guy is doing with the potato: The ObjAct stimulus-set depicting human actions on congruent and incongruent objects. *Behavior Research Methods*, 1–15.

Truman, A., & Mudrik, L. (2018). Are incongruent objects harder to identify? The functional significance of the N300 component. *Neuropsychologia*, 117, 222–232. Underwood, G., & Foulsham, T. (2006). Visual saliency and semantic incongruency influence eye movements when inspecting pictures. *The Quarterly Journal of Experimental Psychology*, 59(11), 1931–1949.

Underwood, G., Humphreys, L., & Cross, E. (2007). Congruency, saliency and gist in the inspection of objects in natural scenes. In Eye Movements (pp. 563-VII). Elsevier.

Underwood, G., Templeman, E., Lamming, L., & Foulsham, T. (2008). Is attention necessary for object identification? Evidence from eye movements during the inspection of real-world scenes. *Consciousness and Cognition*, 17(1), 159–170.

Van Hooff, J. C., Devue, C., Vieweg, P. E., & Theeuwes, J. (2013). Disgust-and not fear-evoking images hold our attention. Acta psychologica, 143(1), 1–6.

Van Hooff, J. C., van Buuringen, M., El M'rabet, I., de Gier, M., & van Zalingen, L. (2014). Disgust-specific modulation of early attention processes. Acta Psychologica, 152, 149–157.

Virtanen, P., Gommers, R., Oliphant, T. E., Haberland, M., Reddy, T., Cournapeau, D., ... van Mulbregt, P. (2020). SciPy 1.0: Fundamental algorithms for scientific computing in Python. Nature Methods, 17(3), 261–272.

Vo, M. L. H., & Henderson, J. M. (2009). Does gravity matter? Effects of semantic and syntactic inconsistencies on the allocation of attention during scene perception. Journal of Vision, 9(3).

Vo, M. L. H., & Henderson, J. M. (2011). Object-scene inconsistencies do not capture gaze: Evidence from the flash-preview moving-window paradigm. Attention, Perception, & Psychophysics, 73(6), 1742–1753.

Vo, M. L. H., & Wolfe, J. M. (2013). Differential electrophysiological signatures of semantic and syntactic scene processing. Psychological science, 24(9), 1816–1823.

Vô, M. L. H., Boettcher, S. E., & Draschkow, D. (2019). Reading scenes: How scene grammar guides attention and aids perception in real-world environments. Current Opinion in Psychology, 29, 205–210.

Wetzels, R., Matzke, D., Lee, M. D., Rouder, J. N., Iverson, G. J., & Wagenmakers, E. J. (2011). Statistical evidence in experimental psychology: An empirical comparison using 855 t tests. *Perspectives on Psychological Science*, 6(3), 291–298.

Wheaton, M. G., Holman, A., Rabinak, C. A., MacNamara, A., Proudfit, G. H., & Phan, K. L. (2013). Danger and disease: Electrocortical responses to threat-and disgusteliciting images. International Journal of Psychophysiology, 90(2), 235–239.

Wolfe, J. M., & Horowitz, T. S. (2017). Five factors that guide attention in visual search. Nature Human Behaviour, 1(3), 1-8.

Wu, C. C., Wick, F. A., & Pomplun, M. (2014). Guidance of visual attention by semantic information in real-world scenes. Frontiers in Psychology, 5, 54.

Zivony, A., & Lamy, D. (2014). Attentional engagement is not sufficient to prevent spatial capture. Attention, Perception, & Psychophysics, 76(1), 19–31.
Publication 2

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CO-AUTHOR'S STATEMENT

As the first author of the article:

Doradzińska, Ł., & Bola, M. (2023). I focus only when I see your fear—fearful faces are not prioritized by attention when processed outside of awareness. *Cerebral Cortex*, *33*(15), 9233–9249.

I declare that my contribution to this publication included:

- participation in the development of the research concept

- critical analysis of existing literature

- development of the experimental procedure

- preparation of EEG equipment and experimental room

- preparation of PRESENTATION scripts for the presentation of visual stimuli which included stimulus sequence randomization and sending the triggers to the EEG signal amplifier

- preparation of visual stimuli (properly cropped face images and masks) establishing shape, luminance and contrast

- recruitment of participants and fulfilling all formal requirements related to their

participation in the study

- conducting all experiments with EEG signal recording

- preparation of PYTHON scripts used for behavioral and electrophysiological data analysis

- electrophysiological data preprocessing and extraction of ERP amplitudes
- selection of statistical tools suitable for data analysis
- preparation of R scripts used for statistical analysis
- statistical analysis of ERP amplitudes employing mixed models
- analysis of behavioral data
- interpretation and discussion of obtained results

- preparation of the initial version of the manuscript
- preparation of all of the figures included in the publication
- participation in correcting and complementing the final version of the manuscript

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I focus only when I see your fear—fearful faces are not prioritized by attention when processed outside of awareness

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The defensive reaction to threats consists of two components: non-specific physiological arousal and specific attentional prioritization of the threatening stimulus, both of which are assumed by the so-called "low-road" hypothesis to be induced automatically and unconsciously. Although ample evidence indicates that non-specific arousal can indeed be caused by unconscious threatening stimuli, data regarding the involvement of the attentional selection mechanism remain inconclusive. Therefore, in the present study we used ERPs to compare the potential engagement of attention in the perception of subliminal and supraliminal fearful facial expressions to that of neutral ones. In the conscious condition, fearful faces were preferentially encoded (as indicated by the N170 component) and prioritized by bottom-up (EPN) and spatial attention (N2pc) in an automatic, task-independent manner. Furthermore, conscious perceived fearful expressions engaged cognitive resources (SPCN, P3) when face stimuli were task-relevant. In the unconscious condition, fearful faces were still preferentially encoded (N170), but we found no evidence for any type of attentional prioritization. Therefore, by showing that threatening stimuli engage attention only when perceived consciously, our findings challenge the "low road" hypothesis and point to the limits of unconscious attentional selection.

Key words: fearful faces; attention; unconsciousness; ERP.

Introduction

A quick and effective reaction to potential danger is a prerequisite for survival in a complex and unpredictable environment. Thus, a widely accepted model of fear reaction assumes that our brains have evolved a so-called defensive survival circuit (LeDoux 2012)—a highly encapsulated, subcortical system that includes structures such as the superior colliculus, the pulvinar, and the amygdala. The role of this circuit is to initiate a defensive reaction rapidly, automatically, and independently of conscious recognition (LeDoux 1998, 2012; Liddell et al. 2005; Öhman et al. 2007; Tamietto and De Gelder 2010; Garrido et al. 2012; LeDoux and Brown 2017). Such an automatic defensive reaction has two postulated components; the first is an increase in general, non-specific arousal (LeDoux 2012; LeDoux and Brown 2017); the second is automatic prioritization of the threat-related stimuli by attention (Phelps 2006; Carlson et al. 2009b; Troiani et al. 2014; LeDoux and Brown 2017). There is indeed robust evidence that subliminal threatening stimuli evoke amygdala activations (Whalen et al. 1998; Morris et al. 1999; Williams et al. 2004a; Williams et al. 2004c; Liddell et al. 2005; Pegna et al. 2005; Williams et al. 2006; Carlson et al. 2009b; Diano et al. 2017) and lead to autonomic nervous system responses (Esteves et al. 1994; Gläscher and 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). However, it is a matter of ongoing debate as to whether the second component of this defensive behavior, namely selective attentional prioritization of the threat-related stimulus, can also be triggered outside of awareness.

Initial evidence provided by behavioral studies has suggested that attentional prioritization of potential threats is indeed automatic and independent of consciousness. For instance, threat-related stimuli have been shown to be more resistant to inattentional blindness (a condition of perceptual unawareness caused by the unavailability of attentional resources) when compared with neutral stimuli. It was demonstrated both, in patients with hemispatial neglect, in whom attentional resources were depleted by brain lesions (Vuilleumier and Schwartz 2001), as well as in healthy participants, whose attentional resources were drawn away from the stimulus by an experimental manipulation (Milders et al. 2006; Maratos et al. 2008; Rosa et al. 2014). Other studies have found that threatening images gain preferential access to consciousness when they are presented to the nondominant eye and compete for attentional resources with other non-threatening stimuli (binocular rivalry, BR) or noise stimuli (continuous flash suppression, CFS) presented to the dominant eye (Yang et al. 2007; Bannerman et al. 2008; Ritchie et al. 2011; Gerdes and Alpers 2014). In other studies, unconscious threatening stimuli modulated reaction times (RTs) to the subsequent target stimuli in the masked visual probe (MVP) paradigm and were thus considered to capture and engage spatial attention (Mogg and Bradley 1999; Fox 2002; Carlson and Reinke 2008; Carlson et al. 2009a; Carlson and Mujica-Parodi 2015; Carlson et al. 2016). Finally, the discovered anatomical and

functional coupling of the amygdala to attention-related cortical areas, such as the anterior cingulate and the prefrontal cortex, has been considered a putative mechanism of the unconscious attentional prioritization of threatening stimuli (Pessoa 2008; Tamietto and De Gelder 2010; Carlson et al. 2013, 2014).

However, despite extensive evidence supporting the unconscious attentional prioritization of threats, there are also studies challenging this claim. A recent meta-analysis conducted by Hedger et al. (2016) found that pooled attentional bias effects observed in studies investigating unconscious threat perception with the BR, CFS, and MVP paradigms are small or even inconsistent. This suggests that the majority of analyzed studies collected insufficient sample sizes, thus the reported significant effects might have been rather incidental. Moreover, Hedger et al. (2016) quite strikingly pointed out that many studies investigating unconscious attentional bias to threats did not test whether the employed awareness suppression method was successful. Considering that studies applying more restrictive masking procedures failed to provide evidence for attentional prioritization of threats (Koster et al. 2007; Hedger et al. 2015a; Hedger et al. 2019), it is highly likely that the "unconscious" attentional bias observed in many previous studies was caused by residual awareness of presented stimuli (see also: Pessoa et al. 2005; Szczepanowski and Pessoa 2007; Lähteenmäki et al. 2015; Mudrik and Deouell 2022).

In the face of inconclusive behavioral results, neuroimaging techniques might provide more reliable data regarding the scope of unconscious reaction to danger. Specifically, EEG event-related potentials (ERPs) seem to be perfectly suited to investigating unconscious attentional prioritization as they provide robust markers of early perceptual and cognitive processes (Luck 2014). Several studies have indeed demonstrated that subliminal threatening stimuli enhance the amplitude of the N2 component, which is a mid-latency, negative potential observed in the frontal brain areas and is considered an indicator of bottomup attentional selection (Liddell et al. 2004; Williams et al. 2004b; Kiss and Eimer 2008; Pegna et al. 2011). Other researchers found that unconscious threats increase the amplitude of the Early Posterior Negativity (EPN) component, which is observed at the posterior brain regions and is interpreted as a marker of bottomup attention (Jiang et al. 2009; Qiu et al. 2023). Furthermore, subliminal threatening stimuli have even been shown to enhance the P3 component, which is typically associated with complex, higher-order cognition (Balconi and Mazza 2009; Wang et al. 2016). However, ERP results are also inconsistent as, for instance, Wang et al. (2016) found that invisible threatening stimuli evoked a decreased amplitude N2 in comparison to neutral stimuli, whereas Jiang et al. (2018) reported that subliminal perception of threats was related to decreased P3 amplitude. What is more, multiple ERP studies have failed to find any effects that can be interpreted as attentional prioritization of unconscious threat-related stimuli (Pegna et al. 2008; Smith 2012; Del Zotto and Pegna 2015; Grassini et al. 2016; Schlossmacher et al. 2017; Qiu et al. 2022). Thus, similarly to the previously discussed behavioral work, the ERP research also seems to provide conflicting or inconclusive results.

Therefore, the aim of the present study was to test the prediction that threat-related stimuli are prioritized by attention even in the absence of awareness (LeDoux and Brown 2017). To provide conclusive evidence either for or against the prioritization effect, our study was designed in the following way. First, the sample size, which had to attain a statistical power of 95%, was estimated based on the meta-analysis conducted by Hedger et al. (2016). Second, considering that fearful faces cause more robust attention-related effects than all other threat-related stimuli

(Hedger et al. 2016), we used images of faces with fearful facial expressions as stimuli in the present study to maximize the chances of finding the effect. Third, to exclude the possibility that our findings could be explained by residual perceptual awareness, the face images were displayed briefly and backward masked, and we controlled the level of stimulus visibility using the objective measure of stimulus recognition. Fourth, taking into account that various attentional mechanisms might be differently involved in the processing of threats, we designed an experimental procedure that allowed investigating both, the general attentional prioritization of fearful faces, as well as orienting of the spatial attention toward them. Fifth, because both the conscious and unconscious processing of threat signals might depend on the task-related context (Zald 2003; Wang et al. 2016; Brown et al. 2020), our procedure comprised two tasks: an identification (ID) task in which face images constituted task-relevant targets (and which allowed us to measure participants' ability to recognize emotional expressions of presented faces), and an adaptation of a standard dot-probe (DP) task (MacLeod et al. 1986) in which faces were presented as task-irrelevant distractors. Finally, we used ERPs as our primary measure of interest as they are more sensitive than behavioral measures (Schmukle 2005; Kappenman et al. 2014) and allow the cortical response to invisible threats to be tracked directly and in a time-resolved manner. The analysis of ERP components was conducted in a single-trial approach to maximize the statistical power of our study and account for interindividual variance. To provide an exhaustive characterization of how unconscious threat signals are processed, in our study we analyzed all components that have been reported to be sensitive to unconscious threat-related stimuli or to consciously perceived fearful faces (for review see: Olofsson et al. 2008; MacNamara et al. 2013; Torrence and Troup 2018; Gupta et al. 2019; Schindler and Bublatzky 2020).

To address our research question, we analyzed the following ERP components. First, the early P1 component, which reflects the processing of the low-level perceptual properties of the stimulus (Di Russo et al. 2002; Jeffreys and Axford 1972); second, the facespecific N170 component, which indexes face encoding (Bentin et al. 1996; Eimer 2000) and classification of emotional expressions (Blau et al. 2007; Hinojosa et al. 2015); third, mid-latency components, namely P2, frontal N2 (sometimes referred to as N2b, Carretié et al. 2004) and EPN (often described also as posterior N2 or N2c; Schupp et al. 2004), which are considered to indicate bottom-up attentional prioritization; fourth, the lateralized N2pc component (N2 posterior contralateral), which marks shifts of spatial attention focus (Luck and Hillyard 1994; Woodman and Luck 2003); finally, the P3 component (Polich 2007, 2012) and the lateralized SPCN potential (sustained posterior contralateral negativity; Jolicœur et al. 2008; Sessa et al. 2011), which reflect the engagement of strategic higher-level cognitive processing, including working memory, sustained attention, and cognitive control (for a review of the attention-related ERP components see: Luck 2012).

We hypothesized that the amplitude of the P1 component would not differ between fearful and neutral faces, thus indicating no difference at the early perceptual stage. However, in both masking conditions and tasks, we expected to observe a difference between expressions when analyzing the amplitude of the N170 component (Pegna et al. 2008; Pegna et al. 2011; Del Zotto and Pegna 2015; but see Qiu et al. 2022). In addition, we expected that fearful faces would evoke greater amplitude of mid-latency and late attention-related components in the conscious condition, with the mid-latency effects being task-independent and the late effects occurring only when faces are task-relevant. In the unconscious condition, we considered two possible outcomes: either similar effects as in the conscious condition, which would indicate that attentional prioritization of threats occurs preconsciously; or finding that fearful and neutral faces do not differ in terms of the amplitude of attention-related components, which would suggest that attentional bias to threatening stimuli requires awareness.

Materials and methods Participants

The sample size for the present study was estimated based on a meta-analysis of behavioral effects reported for fearful faces in the MVP paradigm (Hedger et al. 2016). The estimated effect size (dz=0.58; Hedger et al. 2016) indicated that a group of 41 participants is required to attain a statistical power of 95% (Hedger et al. 2019). We assumed that the sample size estimated from behavioral data should be sufficient to reveal ERP indexes of attentional prioritization, as ERPs measure cognitive mechanisms more directly and in a time-resolved manner.

Data from 41 adult participants were collected (20 females, mean age = 26.9 years, standard deviation = 5.1 years, range: 18–40 years, 1 lefthanded). None of the collected data sets was excluded from the analysis. All participants declared normal or corrected-to-normal vision and no history of mental or neurological disorders. Participants provided written informed consent prior to the experiment and were compensated for their time (150 PLN = ca. 33 EUR). All experimental procedures were approved by the Research Ethics Committee at Nicolaus Copernicus University (KB 447/2020).

Stimuli

In the present study, we used photographs of fearful and neutral faces from the NimStim set of facial expressions (Tottenham et al. 2009). We selected eight female and eight male Caucasian models; for each of these, we chose two pictures: one with a neutral and one with a fearful facial expression (id's of selected pictures: 02F_NE_C, 02F_FE_O, 03F_NE_C, 03F_FE_O, 05F_NE_C, 05F_FE_O, 06F_NE_C, 06F_FE_O, 07F_NE_C, 07F_FE_O, 08F_NE_C, 08F_FE_O, 09F_NE_C, 09F_FE_O, 10F_NE_C, 10M_FE_O, 20M_NE_C, 20M_FE_O, 21M_NE_C, 21M_FE_O, 24M_NE_C, 24M_FE_O, 25M_NE_C, 25M_ FE_O, 27M_NE_C, 27M_FE_O, 28M_NE_C, 28M_FE_O, 33M_NE_C, 33M_FE_O, 34M_NE_C, 34M_FE_O.). Importantly, the NimStim set provides two variants of each facial expression: one with open and another with closed mouths. We used fearful faces with open mouths and neutral faces with closed mouths based on two assumptions: first, an open mouth is an inherent feature of a fearful expression; second, our aim was to obtain the highest clarity and distinctiveness of the presented emotions to test the limits of unconscious fear reaction. These photos of faces were cropped in an oval shape (i.e. without hair) so that the location of significant face elements (eyes, nose, and mouth) was constant between photographs. Next, the stimuli were converted to grayscale and normalized in terms of luminance and contrast using the lum-Match function from the SHINE toolbox (Willenbockel et al. 2010).

A set of 16 "masks" was used to backward mask face stimuli during the procedure. These masks were created in GIMP software by manually cutting rectangular pieces from the original face image, then copying and relocating them (similarly to our previous work: Wójcik et al. 2019; Bola et al. 2021). Only neutral faces were used to create the masks to prevent the influence of perceptually significant components of the masks on the perception of face stimuli. The low-level visual features (e.g. luminance and contrast) were equalized between the masks and the face images using the *lumMatch* SHINE function (Willenbockel et al. 2010).

Procedure

Stimuli were displayed on an LCD monitor DELL AW2518HF (24.5") with 1,920 \times 1,080 resolution (89.91 ppi) and 120 Hz refresh rate. The experimental procedure was programmed and presented using Presentation software (Version 20.1, Neurobehavioral Systems, Inc, Berkeley, CA, www.neurobs.com). Participants were seated in a dimly lit and sound-attenuated room. The viewing distance of 60 cm was maintained by an adjustable chinrest.

All stimuli were presented against a gray background (RGB [128, 128, 128]; Fig. 1). A white fixation cross (Arial, 48 pt font size, 0.8×0.8 cm actual size, $0.8^{\circ} \times 0.8^{\circ}$ of visual angle) was displayed in the center of the screen for the whole duration of the procedure (excluding breaks and instruction displays). Each trial started with the presentation of two oval faces appearing on opposite sides of the screen and remaining there for 16.7 ms. The ovals were scaled to the size of 6.95 cm \times 10.15 cm (6.6° \times 9.6° of visual angle) and displayed with their inner edge at a distance of 4.13 cm (3.9° of visual angle) from the left and right of the fixation cross. Each face could express either a fearful or a neutral emotional state, resulting in four equally frequent combinations: two fearful faces, fearful on the left and neutral on the right, fearful on the right and neutral on the left, or two neutral faces. In half of the trials, the faces were immediately followed by a pair of masks (masked condition), displayed for 50 ms and covering the exact area of face presentation. The faces and masks always came from four different yet gender-matched models. In the other half of trials (unmasked condition), an empty screen was shown instead of the masks. Finally, 500 ms after the masks, a pair of white asterisks (Arial, 60 pt font size, actual size of 0.68 \times 0.64 cm) appeared for 150 ms. The asterisks were arranged either vertically or horizontally, with 1.70 cm distance between them (1.6° of visual angle); they were displayed either on the left or on the right side of the screen, with the middle point between them being in the same location as the center of one of the previously displayed faces (distance of 7.06 cm from the center of the screen, 6.7° of visual angle). The trial ended when the participant responded, or 5 s after presentation of the asterisks.

The experiment consisted of two tasks: a DP task and an ID task. The tasks were introduced in two separate blocks, with the order of blocks counterbalanced across participants. In the DP task, participants had to indicate the arrangement of the presented asterisks (i.e. vertical or horizontal), therefore the faces were task-irrelevant. In the ID task, participants had to indicate the expression of the face that was followed by the pair of asterisks (i.e. the face displayed on the same side of the screen as the asterisks; thus, the faces were task-relevant targets). In both tasks, participants were instructed to respond as fast as possible. Participants responded with a button press using their left and right forefingers. Response mapping in both the DP task and the ID task was counterbalanced across participants.

During each task, participants were presented with 18 sequences of 32 trials, with random trial-to-trial intervals of 1–2 s. After each sequence, participants took a self-paced break. The following factors were balanced within each sequence: gender of faces, the emotional expression of each face, masking condition, on which side of the screen the asterisks were presented, and the



Fig. 1. 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.

orientation of the asterisks. Each combination of these factors was presented exactly once within each sequence in random order. Therefore, the number of trials was 576 per task (18×32), and 1,152 in total.

Behavioral analysis

Analysis of behavioral data was conducted using custom-made Python scripts. Trials in which no response was provided were excluded from the analysis. The median number of retained and analyzed trials was 1,147 (*range* = [1,019, 1,152]) per participant.

Data from the ID task were analyzed using the signal-detection theory (SDT) framework (Wickens 2001). The d' sensitivity measure was calculated to estimate the ability of participants to discriminate facial expressions in the masked and unmasked conditions. Extreme values of the d' parameter were corrected using the "1/(2 N) rule" (Hautus 1995). To assess whether participants exhibited any bias toward one of the responses, we calculated the c parameter, which is interpreted as the locus of the subjective criterion (Wickens 2001). In our study, negative c values indicate a bias toward "fearful" responses; positive c values indicate a bias toward "neutral" responses. The obtained values of d' and the criterion parameter were both statistically tested against 0. D' index equal to zero indicates a chance-level performance of discriminating between the two stimulus types and thus no conscious perception. Criterion equal to zero points to a lack of bias toward any particular response.

In the analysis of DP task data, we investigated how the RTs of manual responses depend on the masking condition, the emotional expression of the face that was followed by the pair of asterisks, and the expression of the second face that was presented on the opposite side of the screen. In the analysis, we included only trials in which a response was correct and was provided 200–1,600 ms after presentation of the asterisks. From each participant and condition, the median RT was calculated and used in the statistical analysis. Importantly, the long interval (over 500 ms) between the face stimuli and presentation of the asterisk introduced in our procedure was not optimal to detect the RT effect in the visual probe task. In addition, the accuracy of responses to the target asterisks was calculated as the percentage of correct responses. The obtained values are presented in the Results section; however, due to the ceiling level performance in the majority of participants, this measure was not analyzed statistically.

EEG recording and analysis

The EEG signal was continuously recorded during the experimental procedure with 64 Ag-AgCl electrically shielded electrodes (Biosemi Active-electrodes) mounted on an elastic cap (Biosemi) and positioned according to the extended 10-20 system. Two referential electrodes (Flat-Type Active-electrodes, BioSemi) were located on the left and right earlobes. The vertical electrooculogram (VEOG) and the horizontal electrooculogram (HEOG) were recorded using bipolar electrodes (Flat-Type Active-electrodes, BioSemi) placed at the supra- and sub-orbit of the right eye and at the external canthi. Data were recorded in a Biosemi "zero-ref" setup using a Common Mode Sense active electrode on the left and a Driven Right Leg passive electrode placed in the elastic cup between the Pz and POz channels on the right side. Impedances of all electrodes were kept below 10 k Ω . The raw, unreferenced signal was amplified and digitized at 2,048 Hz sampling rate by an ActiveTwo AD-box (BioSemi). Data were saved with BioSemi software.

Off-line analysis of the EEG and EOG signals was performed using the MNE 0.24.1 package (Gramfort et al. 2013, 2014) for Python 3.7. First, the EEG data were re-referenced to the algebraic average of the signal from the left and right earlobes. The EOG signals were subtracted within each pair of bipolar electrodes to form two new channels representing vertical and horizontal eye movements. Next, the data were band-pass filtered from 0.1 to 40 Hz (-6 dB cutoff) using a zero-phase FIR filter with a Hamming window (filter() method of Raw object in MNE package; Widmann et al. 2015). Furthermore, the continuous signal was segmented into 1,400 ms long epochs (from -200 ms to 1,200 ms, with respect to the onset of face images). In each epoch, the signal from each channel was baseline-corrected against the mean voltage during the 200 ms pre-stimulus period and then resampled to 256 Hz. At this point, no-response trials and anticipatory-response (i.e. preceding onset of asterisk) trials were rejected from further analysis (median number of rejected trials: 5 out of 1,152 (range = [0, 125]). In the next step, trials with HEOG maximum peak-to-peak signal amplitude exceeding 80 μ V in the 0–500 ms time-window, or with VEOG maximum peak-to-peak signal amplitude exceeding 140 µV in the -100 to 100 ms time-window, were removed. The former criterion was set exclude trials, which contained horizontal eye movements in the time-window in which we would measure lateralized brain responses. The latter criterion was set to exclude trials in which participants blinked during the presentation of face images. To remove the remaining oculomotor artifacts, the EEG signal was decomposed into 64 independent components using Independent Component Analysis (ICA; Makeig et al. 1996). Each independent component was next correlated with the HEOG and VEOG channels (using Pearson correlation), and iterative zscoring with a threshold of 3 was used to repetitively compute the z-scores of components' correlation coefficients in order to identify and remove components with z-scores above the threshold (i.e. further than 3 standard deviations from the mean) until no such components remained in the data (find_bad_eogs() method of ICA object in MNE package). After the ICA decomposition, the EOG channels were excluded from the dataset. As the final step of the artifact rejection procedure, the standardized and automatic procedure implemented in the Autoreject package was applied (Jas et al. 2016, 2017). The Autoreject algorithm calculates the rejection thresholds individually for each participant and each channel (fit() method of the AutoReject object in the Autoreject package; we choose a random search method). Channels exceeding the threshold in a given epoch were rejected and interpolated based on signals from neighboring electrodes. Epochs with too many bad channels were rejected from the dataset (transform() method of the AutoReject object in the Autoreject package; for details of the procedure see Jas et al. 2016, 2017). The number of epochs retained after preprocessing and used in further analysis was, on average, 1043.88 out of 1,152 (range = [653, 1,143]).

ERP analysis

All analyzed ERP components were time-locked to the onset of face images. The signal was averaged across epochs within each condition for visualization purposes only. The following ERP components were examined: P1, N170, P2, N2, EPN, N2pc, SPCN, and P3. The spatio-temporal windows used to analyze each component were defined in the following way. First, topographic maps averaged over all subjects and conditions (Fig. 2A) were used to define clusters of electrodes at which each component reached maximum amplitude. Based on these maps, six temporo-occipital electrodes (P7, P8, PO7, PO8, P9, P10) were chosen for analysis of the P1, N170, and EPN components; six occipital electrodes (PO3, POz, PO4, O1, Oz, O2) were chosen for analysis of the P2 component, six frontal electrodes (F1, F2, Fz, FC1, FC2, FCz) were chosen for frontal N2, and six parietal electrodes (CP1, CPz, CP2, P1, Pz, P2) were chosen for the P3 component. The N2pc and SPCN components were calculated from the temporo-occipital channels (P7, P8, PO7, PO8, P9, P10), according to the literature (for review: Luck 2012). Next, for each ERP component, the time-window was specified based on the visual inspection of waveforms pooled within the chosen cluster of electrodes (Fig.2B). The following time-windows were selected: 80-120 ms for P1, 150-190 ms for N170, 200-250 ms for P2, 200-280 ms for frontal N2, 250-350 ms for EPN, and 350-650 ms for P3. Time-windows for the lateralized components were established based on data from previous studies (Luck 2012), in which N2pc was typically observed in the time-window of the posterior N2 component (in our case EPN), whereas the SPCN component follows N2pc directly. Therefore time-windows specified for those components were: 250-350 ms for N2pc and 350-550 ms for SPCN. Noteworthy, in our study, all spatio-temporal windows were defined independently of the differences in ERP amplitudes caused by the experimental manipulations, to prevent the inflation of the Type I error rate (Keil et al. 2014).

ERP effects were analyzed using hierarchical models. The P1, N170, P2, frontal N2, EPN, and P3 components were analyzed for the effect of emotional content (fearful vs neutral expression) on their amplitude. Thus, these components were estimated from trials containing either two neutral or two emotional faces. To extract the amplitude of a particular component, we calculated the mean potential recorded on the predefined electrodes, within a given time-window, for each trial separately. Next, values obtained from all participants were pooled together, creating an array consisting of 21,359 data points (each data point corresponding to one experimental trial). Each ERP component entered the statistical analysis. Lateralized components (N2pc and SPCN) were analyzed as markers of spatial attention orienting to fearful faces presented on one side of the visual field. Thus, only trials containing one neutral face and one fearful face were included when calculating these two components. For each trial, we calculated the mean amplitudes recorded in a given time-window on the ipsilateral and contralateral electrodes with respect to the side on which the fearful face was presented. Values pooled together across participants resulted in sets of 42,880 data points each (corresponding to the total number of 21,440 analyzed epochs), which were introduced into the statistical models.

Statistical analysis

The statistical tests that were used to evaluate the behavioral results were performed using the open-source JASP 0.25 (JASP Team 2021) software. The SDT parameters obtained in the ID task were described with means (M) and standard deviations (SDs) and were tested against zero with the one-sample t-test. The statistic was reported as t(df), together with Cohen's d measure of effect-size (d). Subject-level median reaction-times collected in DP task were analyzed with a repeated-measures type III ANOVA with three two-level factors: cue (emotion on the face followed by asterisks; neutral or fearful), trial type (symmetric, when both faces expressed the same emotion, or unsymmetric when faces expressed different emotions), and masking (masked or unmasked condition). The outcome of the analysis was reported as F(df); partial eta-squared (the indicator of the effect size) was reported as η_p^2 . For all tests, probability values were reported as P, and the threshold alpha level for refuting the null hypothesis was set to the standard 0.05.

ERP effects were statistically evaluated using mixed linear models. The analysis was conducted in RStudio 1.4.1717 (RStudio Team 2021), which is an open-source software based on the R programming language (R Core Team 2021). Mixed linear models were fitted to ERP data using the "lme4" package (Bates et al. 2015b) and were evaluated with the "lmerTest" package (Kuznetsova et al. 2017) and the "emmeans" package (Lenth 2022). Before fitting the model, trials in which components' amplitudes exceeded three standard deviations from the mean were excluded from each dataset (<0.8% of values).

In the models used to analyze the P1, N170, P2, EPN, frontal N2, and P3 components, the fixed-effects structure contained three two-level factors: *emotion* (fearful or neutral), *task-relevance* (relevant or irrelevant; trials from the ID or DP tasks, respectively), and *masking* (masked or unmasked condition). The models fitted to the lateralized components (N2pc, SPCN) had the same $2 \times 2 \times 2$ fixed-effects design, but instead of *emotion* we included a factor of side (amplitude obtained ipsilaterally or contralaterally



Fig. 2. ERP waveforms averaged over all stimuli types, masking, and task conditions. A) Topographic maps of ERPs in the 60–480 ms time-window. B) ERPs time-locked to the onset of face images. The panels depict ERP waveforms averaged over the following electrodes: upper left—P7, P8, P07, P08, P9, P10; upper right—F1, F2, Fz, FC1, FC2, FCz; lower left—P03, P02, P04, O1, Oz, O2; lower right—CP1, CP2, CP2, P1, Pz, P2. The schematic drawing of the head near each panel depicts the locations of the channels, which were averaged to obtain the ERP waveform. The time-windows chosen for analysis of the components of interest are highlighted in gray.

with respect to the side of fearful face presentation). The randomeffect structure was specified separately for each component, starting with the maximal model (Barr et al. 2013); the iterative reduction of model complexity was conducted until all linear combinations of remaining random effects were estimated to have non-zero variability (i.e. the fitted models are not singular; Bates, Kliegl et al. 2015a). All models selected in this fashion were significantly better than the model containing only the random intercept (comparison was evaluated based on the Akaike information criterion of the selected model and a random intercept model). Fixed effects were evaluated with a type III ANOVA, and the obtained results were reported as F(df). The follow-up analysis consisted of estimation of marginal means (EMM) to obtain the direction of effects. The interactions were resolved with contrasts, which were calculated using Satterthwaite's method for estimating denominator degrees of freedom (Satterthwaite 1941; Luke 2017), and they were reported as t(df). P-values calculated for more than two contrasts were corrected for multiple comparisons with the Holm-Bonferroni method (Holm 1979).

Results Behavioral results

The SDT parameters obtained in the ID task are presented in Fig. 1B. The *d'* values calculated in the masked condition were generally very low but were significantly higher than zero (M=0.10, SD=0.18, range=[-0.25, 0.50], t(40)=3.80, P<0.001,d=0.59). In the unmasked condition, the *d'* values were higher and were also significantly greater than zero (M=1.49, SD=0.47,range=[-0.07, 2.56], t(40)=20.18, P<0.001, d=3.15). The criterion obtained in the masked condition was significantly higher than zero (M=0.32, SD=0.41, range=[-0.85, 1.73], t(40)=4.89, P<0.001,d=0.76), indicating that participants presented a bias toward "neutral" responses; however, in the unmasked condition, we did not find a significant effect (M=-0.04, SD=0.25, range=[-0.97, 0.28], t(40)=-1.12, P<0.270).

Overall accuracy in the DP task was very high (M=93.27%, SD=4.25%, range=[80.70\%, 99.65\%]). The ANOVA conducted on reaction times collected in the DP task revealed no significant effects involving *emotion*. We found a significant interaction

between trial type and masking (F(1, 40) = 5.70, P = 0.022, η_p^2 = 0.13), and the follow-up contrasts suggested that trials containing two faces with the same expression (either both neutral or both fearful) induced longer response times than trials with two different expressions, but the effect was present only in the masked condition (masked: t(79.90) = 2.16, P = 0.034; unmasked: t(79.90) = -1.27, P = 0.206).

ERP results

ERP results, including the P1, N170, N2, EPN, and P3 components, are presented in Fig. 3, whereas the lateralized N2pc and SPCN components are presented in Fig. 4.

Ρ1

A model containing a random intercept and random slope of *task* was concluded to be best for P1 analysis. The ANOVA conducted on fixed effects revealed no statistically significant results.

N170

For the N170 analysis, a model with random intercept and random slopes of masking and task was chosen. The ANOVA on the fixed effects resulted in a significant main effect of emotion (F(1, 21125.2) = 14.45, P < 0.001); this means that fearful expressions evoked greater amplitude of the N170 component (EMM = $-4.03 \ \mu$ V, $Cl = [-4.96 \ \mu$ V, $-3.10 \ \mu$ V]) than neutral faces (EMM = $-3.70 \ \mu$ V, $Cl = [-4.60 \ \mu$ V, $-2.80 \ \mu$ V]). We did not observe any significant interaction of emotion and other factors.

We conducted the analysis of simple main effects to additionally confirm that the effect induced by emotional expression is present irrespective of the stimulus visibility. We found that in unmasked conditions, fearful faces (EMM = -4.36; CI = [-5.28, -3.44]) evoked significantly higher amplitude of the N170 component (t(21,125) = -3.66, P < 0.001), when compared with neutral faces (EMM = -3.92; CI = [-4.84, -2.99]), but in the masked condition this effect remained at the trend level (t(21,125) = -1.73, P = 0.084; fearful, EMM = -3.70; CI = [-4.66, -2.74]; neutral, EMM = -3.49; CI = [-4.45, -2.53]).

In addition, we obtained a significant main effect of masking (F(1, 40)=6.30, P=0.016), indicating that masked stimuli elicited generally lower amplitudes of N170 (EMM= -3.60μ V, $CI = [-4.55 \mu$ V, -2.64μ V]) than unmasked stimuli (EMM= -4.14μ V, $CI = [-5.06 \mu$ V, -3.22μ V]).

Р2

The model containing random intercept and random slopes of *masking*, *task*, and the interaction between these two factors was selected for P2 analysis. The ANOVA on fixed effects revealed no significant effect of *emotion* or any interaction involving this factor.

Further examination of the ANOVA results revealed a significant main effect of masking (F(1, 39.9) = 30.91, P < 0.001), as well as a main effect of task (F(1, 39.9) = 6.55, P = 0.014) and an interaction between masking and task (F(1, 40.2) = 5.00, P = 0.031). The follow-up analyses indicated that the masked stimuli generally evoked a higher amplitude of the P2 component (EMM = 5.16 μ V, CI = [3.90 μ V, 6.42 μ V]) than unmasked ones (EMM = 3.35 μ V, CI = [2.36 μ V, 4.34 μ V]). Moreover, the analysis of simple main effects revealed that the effect of task was present only in the unmasked condition (masked, t(39.8) = 1.63, P = 0.111; unmasked, t(39.8) = 3.06, P = 0.004), and unmasked stimuli in the DP task evoked higher P2 amplitudes (EMM = 3.91 μ V, CI = [2.86 μ V, 4.97 μ V]) than unmasked stimuli in the ID task (EMM = 2.78 μ V, CI = [1.73 μ V, 3.84 μ V]).

Frontal N2

The frontal N2 component was analyzed with the model containing random intercept, random slopes of masking, task and emotion, and a random slope of interaction between masking and task. The ANOVA performed on fixed effects resulted in a significant two-way interaction between emotion and masking (F(1, 21050.3) = 5.85, P = 0.015), which indicates that the effect evoked by fearful faces differed according to stimulus visibility. However, the following contrasts showed that the differences in frontal N2 amplitudes induced by the emotion of presented faces were not statistically significant in either of the masking conditions (masked: t(131) = -1.24, P = 0.216; unmasked: t(126) = 1.97, P = 0.052).

In addition, we found a significant main effect of masking (F(1, 39.1) = 207.34, P < 0.001) and a significant main effect of task (F(1, 40.1) = 17.68, P < 0.001). Masked faces evoked more negative values of the N2 component than unmasked faces (masked, EMM = -2.00 μ V, CI = [-2.97 μ V, -1.04 μ V]; unmasked, EMM = 1.24 μ V, CI = [0.31 μ V, 2.17 μ V]). Similarly, the face stimuli presented in the DP task produced lower N2 values that in the ID task (DP: EMM = -1.00 μ V, CI = [1.93 μ V, -0.07 μ V]; ID: EMM = 0.24 μ V, CI = [0.31 μ V, 1.23 μ V]).

EPN

The model chosen for the EPN component analysis contained random intercept and random slopes of *masking*, *task*, and the interaction between these two factors. The ANOVA conducted on the fixed effects revealed a significant two-way interaction between *emotion* and *masking* (*F*(1, 21075.6) = 5.51, *P* = 0.019). The follow-up analysis revealed that fearful faces in the unmasked condition evoked higher EPN amplitudes in comparison to neutral faces (t(21,074) = -2.64, *P* = 0.008; fearful, *EMM* = 0.18μ V, *CI* = [-0.14μ V, 0.80 μ V]; neutral, *EMM* = 0.51μ V, *CI* = [-0.12μ V, 1.13 μ V]), but this effect was not found in the masked condition (t(21,074) = -0.69, *P* = 0.490).

At the same time, we found a significant main effect of masking (F(1, 40.3)=212.23, P<0.001), a significant main effect of task (F(1, 40.2)=24.02, P<0.001), and an interaction between these two factors (F(1, 40.7)=33.44, P<0.001). The contrasts that were calculated to establish the exact pattern of effects revealed that unmasked stimuli as well as the stimuli presented in the ID task were related to more-negative values of EPN. Moreover, in the unmasked condition, the task factor had a higher impact on EPN amplitudes (t(40.3)=6.02, P<0.001; ID, EMM=-0.78 μ V, CI=[-1.66 μ V, 0.10 μ V]; DP, EMM=1.47 μ V, CI=[0.97 μ V, 1.97 μ V]) than in the masked condition (t(40.1)=3.12, P=0.003; ID, EMM=2.40 μ V, CI=[1.55 μ V, 3.25 μ V]; DP, EMM=3.40 μ V, CI=[2.72 μ V, 4.08 μ V]).

N2pc

The model selected for the N2pc analysis contained a random intercept and random slopes of *masking* and *task*, as well as of the interaction between *masking* and *task*. The ANOVA conducted on fixed effects resulted in a significant main effect of side (F(1, 42,409) = 15.43, P < 0.001) and a significant two-way interaction between side and *masking* (F(1, 1373.7) = 28.16, P < 0.001). The follow-up contrast analysis indicates that the effect of side was present only in the unmasked condition (t(42,409) = -6.55, P < 0.001); it was not present in the masked condition (t(42,409) = 0.97, P = 0.33). When the faces were unmasked, the potentials registered on the contralateral side of the brain were generally lower (EMM=0.09 μ V, $CI = [-0.57 \ \mu$ V, 0.76 μ V])



Fig. 3. 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, P07, P08, P9, P10 electrodes; in the second row, the ERPs were calculated from averaged PO3, PO2, PO4, O1, O2, O2; in the third row, they are averaged from F1, F2, Fz, FC1, FC2, FC2; and in the fourth row, they are averaged from the CP1, CP2, 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.



Fig. 4. 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 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.

than those measured on the ipsilateral side (EMM=0.72 μ V, CI=[0.52 μ V, 1.38 μ V]).

As for effects that were not related to the faces' emotional expressions, the pattern of results was similar to the one observed for the EPN component. We also obtained significant main effects of masking (F(1, 40) = 195.08, P < 0.001) and task (F(1, 40) = 18.71, P < 0.001), as well as a two-way interaction between these factors (F(1, 40) = 28.11, P < 0.001). The calculated contrasts revealed that the unmasked stimuli evoked generally lower potentials in the N2pc spatio-temporal window. Furthermore, trials presented in the ID task resulted in lower values compared with the DP task, and this effect was greater in the unmasked condition (t(40.1) = 5.62, P < 0.001; ID, $EMM = -0.65 \ \mu$ V, $CI = [-1.55 \ \mu$ V, $0.26 \ \mu$ V]; DP, $EMM = 1.45 \ \mu$ V, $CI = [0.88 \ \mu$ V, 2.03 μ V]) than in the masked condition (t(40.1) = 2.17, P = 0.036; ID, $EMM = 2.50 \ \mu$ V, $CI = [1.67 \ \mu$ V, $3.32 \ \mu$ V]; DP, EMM = 3.20 μ V, $CI = [2.49 \ \mu$ V, $3.92 \ \mu$ V]).

SPCN

The SPCN component was analyzed with the model containing a random intercept and random slopes of masking, task, and the masking x task interaction. The ANOVA extracted for the fixed effects revealed significant two-way interactions between side and masking (F(1, 42,376) = 6.94, P = 0.008), and between side and task (F(1, 42,376)=5.36, P=0.021). The follow-up analysis showed that SPCN had a more negative amplitude at the contralateral electrodes (EMM = 0.45 μ V, CI = [0.89 μ V, 2.01 μ V]) than on the ipsilateral side (EMM = 1.74 μ V, CI = [1.18 μ V, 2.30 μ V]) in the unmasked condition (t(42,376) = -2.98, P = 0.003), but this effect was not found in the masked condition (t(42,376)=0.75,P=0.452). Furthermore, the contralateral electrodes exhibited lower values in the SPCN time-window than the ipsilateral electrodes (contralateral, EMM = 1.93 μ V, CI = [1.22 μ V, 2.36 μ V]; ipsilateral, EMM = 2.20 μ V, CI = [1.49 μ V, 2.90 μ V]), but only in the ID task (ID, t(42,376) = -2.72, P=0.007; DP, t(42,376) = 0.53, P=0.594). We also obtained a main effect of masking (F(1, 40) = 4.79), P = 0.035), thus suggesting that unmasked stimuli generally evoked more negative values of the SPCN component (unmasked, EMM = 1.59 μ V, CI = [1.04 μ V, 2.15 μ V]; masked, EMM = 1.98 μ V, $CI = [1.50 \ \mu V, 2.45 \ \mu V]).$

P3

The model selected for P3 analysis included a random intercept and random slopes of *masking*, *task*, and the interaction of *masking* and *task*. The ANOVA extracted for the fixed effects provided multiple significant effects containing the *emotion* factor: a main effect of *emotion* (F(1, 21072.6) = 17.29, P < 0.001), a two-way interaction of *emotion* and task (F(1, 21072.1) = 15.81, P < 0.001), a two-way interaction of *emotion* and *masking* (F(1, 21075.4) = 13.36, P < 0.001) and, most importantly, a three-way interaction of *emotion*, task, and masking (F(1, 21075.4) = 20.37, P < 0.001). The analysis of contrasts that was conducted to resolve the three-way interaction showed that the P3 amplitude evoked by fearful faces was significantly higher than the P3 amplitude evoked by neutral faces, but only in the unmasked condition of the ID task (t(21,068) = 8.13, *p*_{holm} < 0.001; fearful, *EMM* = 6.32 μ V, *CI* = [5.20 μ V, 7.43 μ V]; neutral, *EMM* = 4.36 μ V, *CI* = [3.24 μ V, 5.47 μ V]). The effect of *emotion* was not found in any other combination of the masking and task conditions (unmasked DP, t(21,075) = -0.34, *p*_{holm} = 1; masked ID, t(21,075) = -0.02, *p*_{holm} = 1; masked DP, t(21,075) = 0.52, *p*_{holm} = 1).

We also found a significant main effect of task (F(1, 40.0) = 103.43, P < 0.001) and a significant interaction between *masking* and task (F(1, 40.9) = 17.02, P < 0.001). Analysis of the marginal means suggested that the amplitude of the P3 component was generally higher in the ID task compared with the DP task, and this difference was greater in the unmasked condition (t(40.2) = -10.04, P < 0.001; ID, EMM = 5.34μ V, CI = [4.25μ V, 6.42μ V]; DP, EMM = 0.15μ V, CI = [-0.40μ V, 0.70μ V]) than in the masked condition (t(39.7) = -8.75, P < 0.001; ID, EMM = 4.45μ V, CI = [3.62μ V, 5.29μ V]; DP, EMM = 0.74μ V, CI = [0.11μ V, 1.38μ V]).

Summary

In summary, the early, perceptual P1 component was not influenced by the emotional expressions of the presented facial stimuli during conscious and unconscious presentations. In contrast, the N170 component, which is considered to reflect face encoding, 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). Considering the early attention-related components, neither P2 nor N2 was sensitive to the emotional expression of face stimuli. Furthermore, the amplitude of the EPN component was enhanced by fearful expressions in the conscious but not in the unconscious condition. A similar pattern of results was obtained for the lateralized N2pc component, which was enhanced in response to fearful face presentation, but only when stimuli were consciously perceived. Finally, the amplitude of the lateralized SPCN and the P3 component, both of which are related to the sustained engagement of cognitive resources, was enhanced only during conscious perception of task-relevant fearful faces.

Discussion

The main aim of the present study was to investigate whether attentional selection and prioritization of threatening stimuli take place at the preconscious processing stage. To this end, we used images of faces with neutral and fearful expressions, which we presented either supra- or subliminally while measuring EEG activity. Importantly, the design of our study allowed us to systematically investigate the role of both spatial attention orienting and general attentional prioritization, and to examine whether the potential attentional engagement is task-dependent. Analysis of ERPs suggested automatic encoding of face images regardless of their visibility, as indexed by the difference in the amplitude of the N170 component between fearful and neutral expressions (i.e. the main effect). However, more thorough analysis (i.e. simple main effects) revealed that the N170 effect in the unconscious condition did not reach the significance level (only the trend level). Thus, although modulation of the N170 component by affective unconscious stimuli has been shown by previous work (Jiang and He 2006; Axelrod et al. 2015; Stein et al. 2021; for review see: Mudrik and Deouell 2022), our data are not fully conclusive on this point. In the context of our study, the N170 effects does provide some evidence that subliminally presented stimuli were processed up to a certain stage (i.e. their processing was not completely suppressed by the backward-masking procedure). Most importantly, we did not find any evidence for unconscious attentional selection or prioritization of fearful faces. Specifically, we did not observe differences in ERP components that index bottom-up attentional selection (P2, N2, EPN components), spatial attention orienting (N2pc component), or engagement of attentional resources (SPCN, P3 components) between subliminally presented fearful and neutral faces. Thus, we conclude that the attentional bias toward threat-related stimuli does not emerge at the preconscious stage of stimulus evaluation.

What further supports our conclusion regarding the lack of unconscious attentional prioritization is that we did observe robust attention-related effects in the conscious condition. Specifically, consciously perceived fearful faces, in comparison to neutral ones, were prioritized at the stages of structural encoding (N170), bottom-up attentional selection (EPN), and spatial attention capture (N2pc), with all these effects being observed irrespective of the task. Furthermore, fearful faces induced greater engagement of attentional resources (SPCN, P3), but this process was contingent on faces being task-relevant. Therefore, the pattern of results observed in the conscious condition, which involved both automatic (i.e. task-independent) and strategic (i.e. task-dependent) attentional prioritization, is consistent within our study and in line with effects reported in the literature (e.g. Schupp et al. 2004; Eimer and 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 and Bublatzky 2020). Importantly, the supraliminal condition can be considered a "positive control" in the context of our work as it demonstrates that our procedure was in principle effective and sensitive; also, the null findings from the subliminal condition cannot be accounted for by a range of unspecific factors (like the participant sample, noisy data, inappropriate data analysis, etc.).

Lack of unconscious attentional prioritization—Theoretical implications

Previous work has shown that subcortical areas of the defensive circuit are robustly activated by threat-related stimuli, even when

presented subliminally (Whalen et al. 1998; Morris et al. 1999; Williams et al. 2004a; Williams et al. 2004c; Liddell et al. 2005; Pegna et al. 2005; Williams et al. 2006; Carlson et al. 2009b; Diano et al. 2017), and the defensive circuit structures are anatomically and functionally coupled to attention-related cortical regions, such as the anterior cingulate and the prefrontal cortex (Pessoa 2008; Tamietto and De Gelder 2010; Carlson et al. 2013, 2014). Based on these observations, the so-called "low-road" hypothesis predicts that perception of threats involves automatic and unconscious attentional selection and engagement (Phelps 2006; Carlson et al. 2009b; Troiani et al. 2014; LeDoux and Brown 2017). Although our study does not speak against an increase in amygdala activity or in general physiological arousal in response to unconscious threats, it does show that the attentional bias to threats is neither preconscious (as revealed by data from the unconscious condition) nor entirely automatic (as even in the conscious condition the late stages of attentional engagement were task-dependent). The former finding is in line with several recent behavioral (Koster et al. 2007; Hedger et al. 2015a, 2019) and electrophysiological studies (Pegna et al. 2008; Del Zotto and Pegna 2015; Grassini et al. 2016; Schlossmacher et al. 2017; Qiu et al. 2022), which also found that threat signals do not engage attention pre-consciously. The finding that attentional bias is not entirely automatic supports the view that contextrelated factors shape the scope of attentional prioritization of threats, and it provides further evidence that top-down processes can influence various stages of fear reaction (Pessoa et al. 2002; Holmes et al. 2003; Pessoa 2005; Silvert et al. 2007; Eimer and Kiss 2008; Brosch and Wieser 2011; Dou et al. 2021; Tipura and Pegna 2022). Collectively, this body of work supports the "many roads" hypothesis, which assumes that reaction to threats is not based on the purely sensory assessment of the stimulus and is not encapsulated; instead, it involves a complex interplay between subcortical and cortical areas and is likely based on fine-grained stimulus evaluation involving conscious perception and top-down attention (Pessoa and Adolphs 2010).

Our findings are also relevant to the ongoing discussion regarding the relation between attention and consciousness (De Brigard and Prinz 2010; Van Boxtel et al. 2010; Cohen et al. 2012a, 2012b; Tsuchiya et al. 2012; Tsuchiya and Koch 2014). Recent studies have demonstrated that salient or relevant stimuli might be prioritized by attention even when presented subliminally, which has been interpreted as evidence for a dissociation between attention and perceptual consciousness (Tallon-Baudry 2012; Wyart et al. 2012; for review see Maier and Tsuchiya 2021). Therefore, it is particularly striking that we did not observe any unconscious attentional effects when using fearful faces as stimuli. Fearful faces are particularly likely to benefit from unconscious attentional prioritization not only because they carry emotional value, but also because perception of faces in general is considered highly automatic (Kanwisher 2000; Kanwisher and Yovel 2006; Crouzet et al. 2010; Richler et al. 2011) and to some extent preconscious (review: Axelrod et al. 2015; Mudrik and Deouell 2022). Indeed, other relevant facial features, such as eye gaze direction (Yokoyama et al. 2013) or self-relevance (Wójcik et al. 2019; Bola et al. 2021), have been shown to influence attention at the preconscious stages of perception. Thus, by providing unexpected evidence that fearful faces do not benefit from unconscious attentional prioritization, our study contributes to the ongoing discussion regarding the capabilities of unconscious processing (Hassin 2013; Hesselmann and Moors 2015; Goldstein and Hassin 2017; Melnikoff and Bargh 2018; Hirschhorn et al. 2021).

ERP research on subliminal perception of threats

Previous ERP studies investigating unconscious fear-related attentional bias provided contradictory results, with some speaking in favor (Liddell et al. 2004; Williams et al. 2004b; Kiss and Eimer 2008; Balconi and Mazza 2009; Jiang et al. 2009; Pegna et al. 2011; Wang et al. 2016; Qiu et al. 2023) but others against attentional prioritization of subliminal threats (Pegna et al. 2008; Smith 2012; Del Zotto and Pegna 2015; Grassini et al. 2016; Schlossmacher et al. 2017; Jiang et al. 2018; Qiu et al. 2022). Several factors could be responsible for the low statistical power of the reported analyses, thus explaining these inconsistent findings. First, most studies, especially older ones, collected sample sizes not exceeding 20 participants (Liddell et al. 2004; Williams et al. 2004b; Kiss and Eimer 2008; Pegna et al. 2008; Jiang et al. 2009; Pegna et al. 2011; Smith 2012; Del Zotto and Pegna 2015; Qiu et al. 2023), which is much smaller than the 41 participants required to attain 95% power (Hedger et al. 2016). Second, the authors of previous studies typically analyzed and reported only a single ERP component that they considered to be an index of attention: either the N2, EPN, or P3 components, all of which indicate general attentional prioritization (Liddell et al. 2004; Williams et al. 2004b; Kiss and Eimer 2008; Pegna et al. 2008; Balconi and Mazza 2009; Jiang et al. 2009; Pegna et al. 2011; Del Zotto and Pegna 2015; Grassini et al. 2016; Wang et al. 2016; Schlossmacher et al. 2017; Jiang et al. 2018; Qiu et al. 2023), or the N2pc component, which indicates spatial attention capture (Qiu et al. 2022). Consequently, the attention-related effects have not been tested (or reported) systematically; additionally, considering the publication bias, the actual rate of null findings might be much larger than is reflected in the existing literature. Third, several studies reporting no preconscious attentional prioritization of fearful faces failed to find the N170 effect (Schlossmacher et al. 2017; Qiu et al. 2022, 2023), which suggests the methods used for awareness suppression might have prevented any unconscious processing (Breitmeyer 2015; Michel 2022; Mudrik and Deouell 2022). Finally, the only ERP study that collected a sample big enough to achieve 95% power used cluster-based permutation tests, which are designed specifically for exploratory analyses and are less sensitive than targeted comparisons; thus, the reported lack of unconscious attentional prioritization of fearful faces might potentially reflect the "type II" error (Schlossmacher et al. 2017). Importantly, when designing the present study, we aimed to address all the discussed shortcomings: we conducted an a priori power analysis, examined all previously reported attention-related ERP components, collected evidence suggesting that the masking procedure suppressed visibility but did not prevent unconscious processing entirely, and performed sensitive statistical comparisons based on a single-trial analysis which accounts for between-subject variability. Therefore, we consider our work the most exhaustive and comprehensive ERP investigation of unconscious threat perception to date.

Limitations and conclusions

Although our study was carefully designed to provide evidence for or against unconscious attentional prioritization of threatrelated signals, several limitations of our approach are worth discussing. First, the d' index indicates that participants' identification of the masked faces was substantially reduced, but they were still able to identify facial expressions with greater than chance-level accuracy. Thus, it is not known whether this effect should be interpreted as emotional "blind-sight" (review: Axelrod et al. 2015, but see: Rajananda et al. 2020), or rather as a result of residual awareness. However, even if participants of our study did have some partial awareness of the masked stimuli, this does not undermine our main conclusion regarding the lack of preconscious attentional prioritization; in fact, in a way this even strengthens our conclusion by showing that even partial awareness is not sufficient to evoke the attentional effect.

Regarding selection of stimuli for our study, all images presenting fearful expressions were characterized by open mouths, while all neutral faces had closed mouths (see Methods). Therefore, one might argue that the effects driven by emotional expressions that we observed are not driven by genuine emotional or semantic saliency but by differences between the low-level visual properties of neutral and emotional expressions (for instance, local contrast; Gray et al. 2013; see also Hedger et al. 2015b). Although this argument cannot be refuted based solely on our data, it is worth mentioning that a recent study conducted by Bruchmann et al. (2023) revealed that the modulation of N170 and EPN amplitudes by fearful faces cannot be explained by local differences in lowlevel visual features of any specific face part, but is rather driven by a holistic perception of facial expression. In our study, we found that fearful and neutral faces did not differ in terms of the P1 component's amplitude, which might suggest that the overall strength of early sensory cortex activations was comparable across different emotional expressions. But importantly, the aim of our study was to address whether attentional bias towards fearful faces occurs in different visibility conditions, and not to resolve which specific features of emotional expressions are responsible for the observed effect. Finally, not finding attentional effects in the unconscious condition when using stimuli that are maximally distinctive in terms of physical features strengthens our conclusion regarding no unconscious attentional prioritization.

What can be considered as a limitation of our study is that the two tasks introduced in the experimental procedure differ not only in terms of the status of the face stimulus (relevant or irrelevant) but also engagement of working memory and general difficulty. Although such differences would be considered confounds when aiming to elucidate the specific neural mechanisms behind task-related effects by contrasting DP and ID trials, the aim of our study was to investigate attentional prioritization of threats by contrasting fearful and neutral expressions in different conditions. Accordingly, the *task* factor was included in the statistical models but was of interest only in relation to the effect of emotional expression (i.e. we interpreted its interactive effects, but not main effects).

Furthermore, aware and unaware trials varied not only in terms of face visibility, but also the presence or absence of masks and the overall duration of visual stimulation. However, similarly to the task effect, the effect of masking was interpreted only in relation to the effect caused by the emotional expression. Of note, in our study, we used masks composed of scrambled elements of faces as such masks were shown to maximize the visibility suppression effect (Costen et al. 1994; Wiens 2006). However, because faces with neutral emotional expression were used to create masks, lack of unconscious attentional bias to fearful faces can be potentially accounted for by the fact that masks not only suppressed the neural response induced by fearful faces but additionally evoked activation patterns characteristic to neutral faces. Therefore, the designed backward masking procedure was rather conservative but it introduced additional limitations to the interpretation of our findings.

Finally, our conclusions are based on the analysis of ERP components, which we interpret as indicating subsequent stages of attentional processing, but our study did not provide any reliable behavioral indexes of attentional prioritization. Specifically, in the conscious condition, we found ERP effects of attentional prioritization of fearful faces, but they were not reflected by the RT or accuracy measures in the DP task. However, when designing the study, our aim was to create two tasks that differed only in terms of the instruction. For this reason, manual responses in the DP task had to be delayed with respect to the target stimulus, thus making it unlikely that the RT effect would be observed. Although this can be considered a limitation, behavioral measures of attentional bias have been shown to suffer from low test-retest consistency (Schmukle 2005; Staugaard 2009) and low internal stability (Schmukle 2005; Staugaard 2009; Waechter et al. 2014; Kappenman et al. 2014; MacLeod et al. 2019; but see Bar-Haim et al. 2010), while ERP indexes such as the N2pc component have been shown to be more reliable (Kappenman et al. 2014; Kappenman et al. 2015; Reutter et al. 2017). Accordingly, our study was designed primarily for ERP measurements.

To conclude, by revealing that threat-related stimuli are not attentionally prioritized at the preconscious processing stage, our work challenges one of the key predictions of the low-road hypothesis (LeDoux and Brown 2017) and motivates further research into developing theoretical models of fear reaction.

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Author contributions

Łucja Doradzińska (Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing—original draft preparation, Visualization); Michał Bola (Conceptualization, Methodology, Validation, Writing review & editing, Supervision, Project administration, Funding acquisition).

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Data availability

The scripts used to run the experimental procedure, and the behavioral and EEG data (raw recordings, cleaned and epoched data, mne. Evoked instances and ERP data in long format, which entered statistical analysis) can be downloaded from the OSF repository (https://osf.io/46cuq/). The Python and R scripts were used for data preprocessing and statistical analysis, and a custom Python package containing all used functions can be downloaded from Github (scripts, https://github.com/Lucja-Doradzinska/ff_prep_scripts; package, https://github.com/Lucja-Doradzinska/ erp_exp_ld).

References

- Axelrod V, Bar M, Rees G. Exploring the unconscious using faces. Trends Cogn Sci. 2015:19(1):35–45. https://doi.org/10.1016/j. tics.2014.11.003.
- Balconi M, Mazza G. Consciousness and emotion: ERP modulation and attentive vs. pre-attentive elaboration of emotional facial expressions by backward masking. Motiv Emot. 2009:33(2): 113–124. https://doi.org/10.1007/s11031-009-9122-8.
- Bannerman RL, Milders M, De Gelder B, Sahraie A. Influence of emotional facial expressions on binocular rivalry. Ophthalmic Physiol Opt. 2008:28(4):317–326. https://doi.org/10.1111/ j.1475-1313.2008.00568.x.
- Bar-Haim Y, Holoshitz Y, Eldar S, Frenkel TI, Muller D, Charney DS, Wald I. Life-threatening danger and suppression of attention bias to threat. Am J Psychiatr. 2010:167(6):694–698. https://doi. org/10.1176/appi.ajp.2009.09070956.
- Barr DJ, Levy R, Scheepers C, Tily HJ. Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang. 2013:68(3):255–278. https://doi.org/10.1016/j.jml.2012.11.001.
- Bates D, Kliegl R, Vasishth S, Baayen H. Parsimonious mixed models. arXiv preprint. 2015a. arXiv:150604967. 10.48550/ arXiv.1506.04967.
- Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015b:67(1):1–48. https://doi. org/10.18637/jss.v067.i01.
- Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. J Cogn Neurosci. 1996:8(6): 551–565. https://doi.org/10.1162/jocn.1996.8.6.551.
- Blau VC, Maurer U, Tottenham N, McCandliss BD. The facespecific N170 component is modulated by emotional facial expression. Behav Brain Funct. 2007:3(1):1–13. https://doi. org/10.1186/1744-9081-3-7.
- Bola M, Paź M, Doradzińska Ł, Nowicka A. The self-face captures attention without consciousness: evidence from the N2pc ERP component analysis. Psychophysiology. 2021:58(4):e13759. https:// doi.org/10.1111/psyp.13759.
- Breitmeyer BG. Psychophysical "blinding" methods reveal a functional hierarchy of unconscious visual processing. Conscious Cogn. 2015:35:234–250. https://doi.org/10.1016/j.concog.2015.01.012.
- Brosch T, Wieser MJ. The (non) automaticity of amygdala responses to threat: on the issue of fast signals and slow measures. J Neurosci. 2011:31(41):14451–14452. https://doi.org/10.1523/ JNEUROSCI.4089-11.2011.
- Brown CR, Berggren N, Forster S. Testing a goal-driven account of involuntary attentional capture by threat. Emotion. 2020:20(4): 572–589. https://doi.org/10.1037/emo0000565.
- Bruchmann M, Mertens L, Schindler S, Straube T. Potentiated early neural responses to fearful faces are not driven by specific face parts. Sci Rep. 2023:13(1):4613. https://doi.org/10.1038/ s41598-023-31752-z.
- Carlson JM, Mujica-Parodi LR. Facilitated attentional orienting and delayed disengagement to conscious and nonconscious fearful faces. J Nonverbal Behav. 2015:39(1):69–77. https://doi.org/10.1007/ s10919-014-0185-1.
- Carlson JM, Reinke KS. Masked fearful faces modulate the orienting of covert spatial attention. *Emotion*. 2008:8(4):522. https://doi. org/10.1037/a0012653.
- Carlson JM, Fee AL, Reinke KS. Backward masked snakes and guns modulate spatial attention. Evol Psychol. 2009a:7(4):534–544. https://doi.org/10.1177/147470490900700404.
- Carlson JM, Reinke KS, Habib R. A left amygdala mediated network for rapid orienting to masked fearful faces.

Neuropsychologia. 2009b:47(5):1386–1389. https://doi.org/10.1016/ j.neuropsychologia.2009.01.026.

- Carlson JM, Cha J, Mujica-Parodi LR. Functional and structural amygdala—anterior cingulate connectivity correlates with attentional bias to masked fearful faces. *Cortex*. 2013:49(9):2595–2600. https://doi.org/10.1016/j.cortex.2013.07.008.
- Carlson JM, Cha J, Harmon-Jones E, Mujica-Parodi LR, Hajcak G. Influence of the BDNF genotype on amygdalo-prefrontal white matter microstructure is linked to nonconscious attention bias to threat. *Cereb Cortex*. 2014:24(9):2249–2257. https://doi.org/10.1093/cercor/bht089.
- Carlson JM, Torrence RD, Vander Hyde MR. Beware the eyes behind the mask: the capture and hold of selective attention by backward masked fearful eyes. *Motiv Emot*. 2016:40(3):498–505. https:// doi.org/10.1007/s11031-016-9542-1.
- Carretié L, Hinojosa JA, Martín-Loeches M, Mercado F, Tapia M. Automatic attention to emotional stimuli: neural correlates. *Hum Brain Mapp*. 2004:22(4):290–299. https://doi.org/10.1002/hbm.20037.
- Cohen MA, Cavanagh P, Chun MM, Nakayama K. The attentional requirements of consciousness. *Trends Cogn Sci.* 2012a:16(8): 411–417. https://doi.org/10.1016/j.tics.2012.06.013.
- Cohen MA, Cavanagh P, Chun MM, Nakayama K. Response to Tsuchiya et al.: considering endogenous and exogenous attention. Trends Cogn Sci. 2012b:16(11):528. https://doi.org/10.1016/j. tics.2012.09.002.
- Costen NP, Shepherd JW, Ellis HD, Craw I. Masking of faces by facial and non-facial stimuli. Vis Cogn. 1994:1(2–3):227–251. https://doi. org/10.1080/13506289408402301.
- Crouzet SM, Kirchner H, Thorpe SJ. Fast saccades toward faces: face detection in just 100 ms. J Vis. 2010:10(4):16–16. https://doi. org/10.1167/10.4.16.
- De Brigard F, Prinz J. Attention and consciousness. Wiley Interdiscip Rev Cogn Sci. 2010:1(1):51–59. https://doi.org/10.1002/wcs.27.
- Del Zotto M, Pegna AJ. Processing of masked and unmasked emotional faces under different attentional conditions: an electrophysiological investigation. Front Psychol. 2015:6:1691. https://doi. org/10.3389/fpsyg.2015.01691.
- Di Russo F, Martínez A, Sereno MI, Pitzalis S, Hillyard SA. Cortical sources of the early components of the visual evoked potential. *Hum Brain Mapp.* 2002:15(2):95–111. https://doi.org/10.1002/ hbm.10010.
- Diano M, Celeghin A, Bagnis A, Tamietto M. Amygdala response to emotional stimuli without awareness: facts and interpretations. Front Psychol. 2017:7:2029. https://doi.org/10.3389/ fpsyg.2016.02029.
- Dou H, Liang L, Ma J, Lu J, Zhang W, Li Y. Irrelevant task suppresses the N170 of automatic attention allocation to fearful faces. *Sci Rep.* 2021:11(1):1–10. https://doi.org/10.1038/s41598-021-91237-9.
- Eimer M. The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*. 2000:11(10): 2319–2324. https://doi.org/10.1097/00001756-200007140-00050.
- Eimer M, Kiss M. Attentional capture by task-irrelevant fearful faces is revealed by the N2pc component. Biol Psychol. 2007:74(1): 108–112. https://doi.org/10.1016/j.biopsycho.2006.06.008.
- Eimer M, Kiss M. Involuntary attentional capture is determined by task set: evidence from event-related brain potentials. J Cogn Neurosci. 2008:20(8):1423–1433. https://doi.org/10.1162/ jocn.2008.20099.
- Esteves F, Dimberg U, Öhman A. Automatically elicited fear: conditioned skin conductance responses to masked facial expressions. *Cogn Emot.* 1994:8(5):393–413. https://doi.org/10.1080/02699939 408408949.

- Fox E. Processing emotional facial expressions: the role of anxiety and awareness. Cogn Affect Behav Neurosci. 2002:2(1):52–63. https://doi.org/10.3758/CABN.2.1.52.
- Garrido MI, Barnes GR, Sahani M, Dolan RJ. Functional evidence for a dual route to amygdala. *Curr Biol.* 2012:22(2):129–134. https://doi.org/10.1016/j.cub.2011.11.056.
- Gerdes ABM, Alpers GW. You see what you fear: spiders gain preferential access to conscious perception in spider-phobic patients. J Exp Psychopathol. 2014:5(1):14–28. https://doi. org/10.5127/jep.033212.
- Gläscher J, Adolphs R. Processing of the arousal of subliminal and supraliminal emotional stimuli by the human amygdala. J Neurosci. 2003:23(32):10274–10282. https://doi.org/10.1523/ JNEUROSCI.23-32-10274.2003.
- Goldstein A, Hassin RR. Commentary: Definitely maybe: can unconscious processes perform the same functions as conscious processes? Frontiers in Psychology. 2017:8:1230. https://doi. org/10.3389/fpsyg.2017.01230.
- Gramfort A, Luessi M, Larson E, Engemann DA, Strohmeier D, Brodbeck C, Hämäläinen MS. MEG and EEG data analysis with MNE-python. Front Neurosci. 2013:7:267. https://doi.org/10.3389/ fnins.2013.00267.
- Gramfort A, Luessi M, Larson E, Engemann DA, Strohmeier D, Brodbeck C, Hämäläinen MS. MNE software for processing MEG and EEG data. *Neuroimage*. 2014:86:446–460. https://doi.org/10.1016/j. neuroimage.2013.10.027.
- Grassini S, Holm SK, Railo H, Koivisto M. Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. Biol Psychol. 2016:121:53–61. https://doi.org/10.1016/j.biopsycho.2016.10.007.
- Gray KL, Adams WJ, Hedger N, Newton KE, Garner M. Faces and awareness: low-level, not emotional factors determine perceptual dominance. *Emotion*. 2013:13(3):537. https://doi.org/10.1037/ a0031403.
- Gupta RS, Kujawa A, Vago DR. The neural chronometry of threatrelated attentional bias: event-related potential (ERP) evidence for early and late stages of selective attentional processing. Int J Psychophysiol. 2019:146:20–42. https://doi.org/10.1016/j. ijpsycho.2019.08.006.
- Hajcak G, MacNamara A, Olvet DM. Event-related potentials, emotion, and emotion regulation: an integrative review. Dev Neuropsychol. 2010:35(2):129–155. https://doi.org/10.1080/87565640 903526504.
- Hamm AO, Schupp HT, Weike AI. Motivational organization of emotions: autonomic changes, cortical responses, and reflex modulation. Oxford: Oxford University Press; 2003.
- Hassin RR. Yes it can: On the functional abilities of the human unconscious. Perspectives on Psychological Science. 2013:8(2):195–207. https://doi.org/10.3389/fpsyg.2016.02029.
- Hautus MJ. Corrections for extreme proportions and their biasing effects on estimated values ofd'. Behav Res Methods Instrum Comput. 1995:27(1):46–51. https://doi.org/10.3758/BF03203619.
- Hedger N, Adams WJ, Garner M. Autonomic arousal and attentional orienting to visual threat are predicted by awareness. J Exp Psychol Hum Percept Perform. 2015a:41(3):798. https://doi.org/10.1037/ xhp0000051.
- Hedger N, Adams WJ, Garner M. Fearful faces have a sensory advantage in the competition for awareness. J Exp Psychol Hum Percept Perform. 2015b:41(6):1748. https://doi.org/10.1037/xhp0000127.
- Hedger N, Gray KL, Garner M, Adams WJ. Are visual threats prioritized without awareness? A critical review and meta-analysis involving 3 behavioral paradigms and 2696 observers. Psychol Bull. 2016:142(9):934. https://doi.org/10.1037/bul0000054.

- Hedger N, Garner M, Adams WJ. Do emotional faces capture attention, and does this depend on awareness? Evidence from the visual probe paradigm. J Exp Psychol Hum Percept Perform. 2019:45(6):790–802. https://doi.org/10.1037/xhp0000640.
- Hesselmann G, & Moors P. Definitely maybe: can unconscious processes perform the same functions as conscious processes? Frontiers in Psychology. 2015:6:584. https://doi.org/10.3389/fpsyg.2015.00584.
- Hinojosa JA, Mercado F, Carretié L. N170 sensitivity to facial expression: a meta-analysis. Neurosci Biobehav Rev. 2015:55: 498–509. https://doi.org/10.1016/j.neubiorev.2015.06.002.
- Hirschhorn R, Kahane O, Gur-Arie I, Faivre N, Mudrik L. Windows of Integration Hypothesis Revisited. Frontiers in Human Neuroscience, 2021:14:617187. https://doi.org/10.3389/fnhum.2020.617187.
- Holm S. A simple sequentially rejective multiple test procedure. Scand J Stat. 1979:6(2):65–70. http://www.jstor.org/stable/4615733.
- Holmes A, Vuilleumier P, Eimer M. The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. Cogn Brain Res. 2003:16(2):174–184. https://doi.org/10.1016/S0926-6410(02)00268-9.
- van Honk J, Tuiten A, van den Hout M, Koppeschaar H, Thijssen J, de Haan E, Verbaten R. Baseline salivary cortisol levels and preconscious selective attention for threat: a pilot study. Psychoneuroendocrinology. 1998:23(7):741–747. https://doi.org/10.1016/ S0306-4530(98)00047-X.
- Jas M, Engemann D, Raimondo F, Bekhti Y, Gramfort A. Automated rejection and repair of bad trials in MEG/EEG. 2016 international workshop on pattern recognition in neuroimaging (PRNI). 2016:1–4. 10.1109/PRNI.2016.7552336.
- Jas M, Engemann DA, Bekhti Y, Raimondo F, Gramfort A. Autoreject: automated artifact rejection for MEG and EEG data. Neuroimage. 2017:159:417–429. https://doi.org/10.1016/j. neuroimage.2017.06.030.
- JASP Team. JASP (version 0.15). Comput Softw. 2021. https://jasp-stats. org/.
- Jeffreys DA, Axford JG. Source locations of pattern-specific components of human visual evoked potentials. I. Component of striate cortical origin. Exp Brain Res. 1972:16:1–21. https://doi. org/10.1007/BF00233371.
- Jiang Y, He S. Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr Biol.* 2006:16(20): 2023–2029. https://doi.org/10.1016/j.cub.2006.08.084.
- Jiang YI, Shannon RW, Vizueta N, Bernat EM, Patrick CJ, He S. Dynamics of processing invisible faces in the brain: automatic neural encoding of facial expression information. *Neuroimage*. 2009:44(3):1171–1177. https://doi.org/10.1016/j. neuroimage.2008.09.038.
- Jiang Y, Wu X, Saab R, Xiao Y, Gao X. Time course of influence on the allocation of attentional resources caused by unconscious fearful faces. *Neuropsychologia*. 2018:113:104–110. https:// doi.org/10.1016/j.neuropsychologia.2018.04.001.
- Jolicœur P, Brisson B, Robitaille N. Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. Brain Res. 2008:1215:160–172. https://doi.org/10.1016/j. brainres.2008.03.059.
- Kanwisher N. Domain specificity in face perception. Nat Neurosci. 2000:3(8):759–763. https://doi.org/10.1038/77664.
- Kanwisher N, Yovel G. The fusiform face area: a cortical region specialized for the perception of faces. Philos Trans R Soc B Biol Sci. 2006:361(1476):2109–2128. https://doi.org/10.1098/ rstb.2006.1934.
- Kappenman ES, Farrens JL, Luck SJ, Proudfit GH. Behavioral and ERP measures of attentional bias to threat in the dot-probe task:

poor reliability and lack of correlation with anxiety. Front Psychol. 2014:5:1368. https://doi.org/10.3389/fpsyg.2014.01368.

- Kappenman ES, MacNamara A, Proudfit GH. Electrocortical evidence for rapid allocation of attention to threat in the dotprobe task. Soc Cogn Affect Neurosci. 2015:10(4):577–583. https:// doi.org/10.1093/scan/nsu098.
- Keil A, Debener S, Gratton G, Junghöfer M, Kappenman ES, Luck SJ, Yee CM. Committee report: publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. Psychophysiology. 2014:51(1):1–21. https:// doi.org/10.1111/psyp.12147.
- Kiss M, Eimer M. ERPs reveal subliminal processing of fearful faces. Psychophysiology. 2008:45(2):318–326. https://doi.org/10.1111/ j.1469-8986.2007.00634.x.
- Koster EH, Verschuere B, Burssens B, Custers R, Crombez G. Attention for emotional faces under restricted awareness revisited: do emotional faces automatically attract attention? *Emotion*. 2007:7(2):285. https://doi.org/10.1037/1528-3542.7.2.285.
- Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects models. J Stat Softw. 2017:82(13):1–26. https://doi.org/10.18637/jss.v082.i13.
- Lähteenmäki M, Hyönä J, Koivisto M, Nummenmaa L. Affective processing requires awareness. J Exp Psychol Gen. 2015:144(2):339. https://doi.org/10.1037/xge0000040.
- LeDoux J. The emotional brain: the mysterious underpinnings of emotional life. New York: Simon and Schuster; 1998.
- LeDoux J. Rethinking the emotional brain. Neuron. 2012:73(4): 653–676. https://doi.org/10.1016/j.neuron.2012.02.004.
- LeDoux J, Brown R. A higher-order theory of emotional consciousness. Proc Natl Acad Sci U S A. 2017:114(10):E2016–E2025. https:// doi.org/10.1073/pnas.1619316114.
- Lenth R. Emmeans: estimated marginal means, aka least-squares means. R package version 1.4.7.2020 July 14. 2022.
- Liddell BJ, Williams LM, Rathjen J, Shevrin H, Gordon E. A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. J Cogn Neurosci. 2004:16(3): 479–486. https://doi.org/10.1162/089892904322926809.
- Liddell BJ, Brown KJ, Kemp AH, Barton MJ, Das P, Peduto A, Williams LM. A direct brainstem–amygdala–cortical 'alarm'system for subliminal signals of fear. *Neuroimage*. 2005:24(1):235–243. https://doi.org/10.1016/j.neuroimage.2004.08.016.
- Luck SJ. Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In: Luck SJ, Kappenman ES, editors. The Oxford handbook of eventrelated potential components. Oxford: Oxford University Press; 2012. pp. 329–360.
- Luck SJ. An introduction to the event-related potential technique. Cambrige: MIT press; 2014.
- Luck SJ, Hillyard SA. Spatial filtering during visual search: evidence from human electrophysiology. J Exp Psychol Hum Percept Perform. 1994:20(5):1000. https://doi.org/10.1037/0096-1523.20.5.1000.
- Luke SG. Evaluating significance in linear mixed-effects models in R. Behav Res Methods. 2017:49(4):1494–1502. https://doi.org/10.3758/ s13428-016-0809-y.
- MacLeod C, Mathews A, Tata P. Attentional bias in emotional disorders. J Abnorm Psychol. 1986:95(1):15–20. https://doi. org/10.1037/0021-843X.95.1.15.
- MacLeod C, Grafton B, Notebaert L. Anxiety-linked attentional bias: is it reliable? Annu Rev Clin Psychol. 2019:15:529–554. https://doi. org/10.1146/annurev-clinpsy-050718-095505.
- MacNamara A, Kappenman ES, Black SR, Bress JN, Hajcak G. 11 integrating behavioral and electrocortical measures of attentional bias toward threat. In: Karen Caplovitz Barrett K, Fox NA, Morgan

GA, Fidler DJ, Daunhauer LA, editors. Handbook of self-regulatory processes in development. New York: Psychology Press; 2013. pp. 215–243.

- Maier A, Tsuchiya N. Growing evidence for separate neural mechanisms for attention and consciousness. Attent Percept Psychophys. 2021:83(2):558–576. https://doi.org/10.3758/s13414-020-02146-4.
- Makeig S, Jung TP, Ghahremani D, Sejnowski TJ. Independent component analysis of simulated ERP data. San Diego: Institute for Neural Computation, University of California; 1996. Technical report INC-9606.
- Maratos FA, Mogg K, Bradley BP. Identification of angry faces in the attentional blink. *Cogn Emot.* 2008:22(7):1340–1352. https://doi.org/10.1080/02699930701774218.
- Melnikoff DE, & Bargh JA. The mythical number two. Trends in cognitive sciences. 2018:22(4):280–293. https://doi.org/10.1016/j. tics.2018.02.001.
- Michel M. How (not) to underestimate unconscious perception. *Mind* Lang. 2022:28(2):413–430. https://doi.org/10.1111/mila.12406.
- Milders M, Sahraie A, Logan S, Donnellon N. Awareness of faces is modulated by their emotional meaning. *Emotion*. 2006:6(1):10. https://doi.org/10.1037/1528-3542.6.1.10.
- Mogg K, Bradley BP. Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cogn Emot.* 1999:13(6):713–740. https://doi.org/10.1080/026999 399379050.
- Morris JS, Öhman A, Dolan RJ. A subcortical pathway to the right amygdala mediating "unseen" fear. Proc Natl Acad Sci U S A. 1999:96(4):1680–1685. https://doi.org/10.1073/pnas.96.4.1680.
- Mudrik L, Deouell LY. Neuroscientific evidence for processing without awareness. Annu Rev Neurosci. 2022:45:403–423. https://doi. org/10.1146/annurev-neuro-110920-033151.
- Öhman A, Carlsson K, Lundqvist D, Ingvar M. On the unconscious subcortical origin of human fear. Physiol Behav. 2007:92(1–2): 180–185. https://doi.org/10.1016/j.physbeh.2007.05.057.
- Olofsson JK, Nordin S, Sequeira H, Polich J. Affective picture processing: an integrative review of ERP findings. Biol Psychol. 2008:77(3): 247–265. https://doi.org/10.1016/j.biopsycho.2007.11.006.
- Pegna AJ, Khateb A, Lazeyras F, Seghier ML. Discriminating emotional faces without primary visual cortices involves the right amygdala. Nat Neurosci. 2005:8(1):24–25. https://doi.org/10.1038/ nn1364.
- Pegna AJ, Landis T, Khateb A. Electrophysiological evidence for early non-conscious processing of fearful facial expressions. Int J Psychophysiol. 2008:70(2):127–136. https://doi.org/10.1016/j. ijpsycho.2008.08.007.
- Pegna AJ, Darque A, Berrut C, Khateb A. Early ERP modulation for task-irrelevant subliminal faces. Front Psychol. 2011:2:88. https:// doi.org/10.3389/fpsyg.2011.00088.
- Pessoa L. To what extent are emotional visual stimuli processed without attention and awareness? Curr Opin Neurobiol. 2005:15(2): 188–196. https://doi.org/10.1016/j.conb.2005.03.002.
- Pessoa L. On the relationship between emotion and cognition. Nat Rev Neurosci. 2008:9(2):148–158. https://doi.org/10.1038/nrn2317.
- Pessoa L, Adolphs R. Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat Rev Neurosci. 2010:11(11):773–782. https://doi.org/10.1038/ nrn2920.
- Pessoa L, McKenna M, Gutierrez E, Ungerleider LG. Neural processing of emotional faces requires attention. Proc Natl Acad Sci U S A. 2002:99(17):11458–11463. https://doi.org/10.1073/pnas. 172403899.

- Pessoa L, Japee S, Ungerleider LG. Visual awareness and the detection of fearful faces. Emotion. 2005:5(2):243. https://doi. org/10.1037/1528-3542.5.2.243.
- Phelps EA. Emotion and cognition: insights from studies of the human amygdala. Annu Rev Psychol. 2006:57:27–53. https://doi.org/10.1146/annurev.psych.56.091103.070234.
- Polich J. Updating P300: an integrative theory of P3a and P3b. Clin Neurophysiol. 2007:118(10):2128–2148. https://doi.org/10.1016/j. clinph.2007.04.019.
- Polich J. Neuropsychology of P300. In: Luck SJ, Kappenman ES, editors. The Oxford handbook of event-related potential components. Oxford: Oxford University Press; 2012. pp. 159–188.
- Qiu Z, Becker SI, Pegna AJ. Spatial attention shifting to emotional faces is contingent on awareness and task relevancy. Cortex. 2022:151:30–48. https://doi.org/10.1016/j.cortex.2022.02.009.
- Qiu Z, Zhang J, Pegna AJ. Neural processing of lateralised task-irrelevant fearful faces under different awareness conditions. Conscious Cogn. 2023:107:103449. https://doi.org/10.1016/j. concog.2022.103449.
- R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2021. URL: https://www.R-project.org/.
- Rajananda S, Zhu J, Peters MA. Normal observers show no evidence for blindsight in facial emotion perception. *Neurosci Conscious*. 2020:2020(1):niaa023. 10.1093/nc/niaa023.
- Reutter M, Hewig J, Wieser MJ, Osinsky R. The N2pc component reliably captures attentional bias in social anxiety. *Psychophysiology*. 2017:54(4):519–527. https://doi.org/10.1111/ psyp.12809.
- Richler JJ, Wong YK, Gauthier I. Perceptual expertise as a shift from strategic interference to automatic holistic processing. Curr Dir Psychol Sci. 2011:20(2):129–134. https://doi. org/10.1177/096372141140247.
- Ritchie KL, Bannerman RL, Sahraie A. The effect of fear in the periphery in binocular rivalry. *Perception*. 2011:40(12):1395–1401. https://doi.org/10.1068/p7157.
- Rosa PJ, Esteves F, Arriaga P. Effects of fear-relevant stimuli on attention: Integrating gaze data with subliminal exposure. 2014 IEEE international symposium on medical measurements and applications (MeMeA). 2014:1–6. https://doi.org/10.1109/MeMeA.2014.6860021.
- RStudio Team. RStudio: integrated development environment for R. Boston, MA: RStudio, PBC; 2021. URL: http://www.rstudio.com/.
- Ruiz-Padial E, Mata JL, Rodríguez S, Fernández MC, Vila J. Nonconscious modulation of cardiac defense by masked phobic pictures. Int J Psychophysiol. 2005:56(3):271–281. https://doi. org/10.1016/j.ijpsycho.2004.12.010.
- Satterthwaite FE. Synthesis of variance. Psychometrika. 1941:6(5): 309–316. 10.1007/BF02288586.
- Schindler S, Bublatzky F. Attention and emotion: an integrative review of emotional face processing as a function of attention. Cortex. 2020:130:362–386. https://doi.org/10.1016/j. cortex.2020.06.010.
- Schlossmacher I, Junghöfer M, Straube T, Bruchmann M. No differential effects to facial expressions under continuous flash suppression: an event-related potentials study. *Neuroimage*. 2017:163: 276–285. 10.1016/j.neuroimage.2017.09.034.
- Schmukle SC. Unreliability of the dot probe task. Eur J Personal. 2005:19(7):595–605. https://doi.org/10.1002/per.554.
- Schupp HT, Öhman A, Junghöfer M, Weike AI, Stockburger J, Hamm AO. The facilitated processing of threatening faces: an ERP analysis. *Emotion*. 2004:4(2):189. https://doi.org/10.1037/1528-3542.4.2.189.

- Sessa P, Luria R, Gotler A, Jolicœur P, Dell'Acqua R. Interhemispheric ERP asymmetries over inferior parietal cortex reveal differential visual working memory maintenance for fearful versus neutral facial identities. Psychophysiology. 2011:48(2):187–197. https://doi. org/10.1111/j.1469-8986.2010.01046.x.
- Silvert L, Lepsien J, Fragopanagos N, Goolsby B, Kiss M, Taylor JG, Nobre AC. Influence of attentional demands on the processing of emotional facial expressions in the amygdala. Neuroimage. 2007:38(2):357–366. https://doi.org/10.1016/j. neuroimage.2007.07.023.
- Smith ML. Rapid processing of emotional expressions without conscious awareness. Cereb Cortex. 2012:22(8):1748–1760. https://doi. org/10.1093/cercor/bhr250.
- Staugaard SR. Reliability of two versions of the dot-probe task using photographic faces. Psychol Sci Q. 2009:51(3): 339–350.
- Stein T, Kaiser D, Fahrenfort JJ, Van Gaal S. The human visual system differentially represents subjectively and objectively invisible stimuli. PLoS Biol. 2021:19(5):e3001241. https://doi.org/10.1371/ journal.pbio.3001241.
- Stewart LH, Ajina S, Getov S, Bahrami B, Todorov A, Rees G. Unconscious evaluation of faces on social dimensions. J Exp Psychol Gen. 2012:141(4):715. https://doi.org/10.1037/a0027950.
- Szczepanowski R, Pessoa L. Fear perception: can objective and subjective awareness measures be dissociated? J Vis. 2007:7(4):10–10. https://doi.org/10.1167/7.4.10.
- Tallon-Baudry C. On the neural mechanisms subserving consciousness and attention. Front Psychol. 2012:2:397. https://doi. org/10.3389/fpsyg.2011.00397.
- Tamietto M, De Gelder B. Neural bases of the non-conscious perception of emotional signals. Nat Rev Neurosci. 2010:11(10):697–709. https://doi.org/10.1038/nrn2889.
- Tamietto M, Castelli L, Vighetti S, Perozzo P, Geminiani G, Weiskrantz L, de Gelder B. Unseen facial and bodily expressions trigger fast emotional reactions. Proc Natl Acad Sci U S A. 2009:106(42): 17661–17666. https://doi.org/10.1073/pnas.0908994106.
- Tamietto M, Cauda F, Celeghin A, Diano M, Costa T, Cossa FM, de Gelder B. Once you feel it, you see it: insula and sensorymotor contribution to visual awareness for fearful bodies in parietal neglect. Cortex. 2015:62:56–72. https://doi.org/10.1016/j. cortex.2014.10.009.
- Tipura E, Pegna AJ. Subliminal emotional faces do not capture attention under high attentional load in a randomized trial presentation. Vis Cogn. 2022:30(4):280–288. https://doi. org/10.1080/13506285.2022.2060397.
- Torrence RD, Troup LJ. Event-related potentials of attentional bias toward faces in the dot-probe task: a systematic review. Psychophysiology. 2018:55(6):e13051. https://doi.org/10.1111/ psyp.13051.
- Tottenham N, Tanaka JW, Leon AC, McCarry T, Nurse M, Hare TA, Nelson C. The NimStim set of facial expressions: judgments from untrained research participants. Psychiatry Res. 2009:168(3): 242–249. https://doi.org/10.1016/j.psychres.2008.05.006.
- Troiani V, Price ET, Schultz RT. Unseen fearful faces promote amygdala guidance of attention. Soc Cogn Affect Neurosci. 2014:9(2): 133–140. https://doi.org/10.1093/scan/nss116.
- Tsuchiya N, Koch C. On the relationship between consciousness and attention. In: Gazzaniga MS, Mangun GR, editors, *The cognitive neurosciences*. Cambrige: MIT Press; 2014. pp. 839–853.
- Tsuchiya N, Block N, Koch C, et al. Top-down attention and consciousness: comment on Cohen. Trends Cogn Sci. 2012:16(11):527. https://doi.org/10.1016/j.tics.2012.09.004.

- Van Boxtel JJ, Tsuchiya N, Koch C. Consciousness and attention: on sufficiency and necessity. Front Psychol. 2010:1:217. https://doi. org/10.3389/fpsyg.2010.00217.
- van Honk J, Tuiten A, van den Hout M, Koppeschaar H, Thijssen J, de Haan E, Verbaten R. Conscious and preconscious selective attention to social threat: different neuroendocrine response patterns. *Psychoneuroendocrinology*. 2000:25(6):577–591. https://doi.org/10.1016/S0306-4530(00)00011-1.
- Vuilleumier P, Schwartz S. Beware and be aware: capture of spatial attention by fear-related stimuli in neglect. Neuroreport. 2001;12(6):1119–1122. https://doi.org/10.1097/00001756-200 105080-00014.
- Waechter S, Nelson AL, Wright C, Hyatt A, Oakman J. Attentional bias to threat in social anxiety: psychometric properties of dot probe and eye-tracking measures. *Cogn Ther Res.* 2014:38:313–333. https://doi.org/10.1007/s10608-013-9588-2.
- Wang L, Feng C, Mai X, Jia L, Zhu X, Luo W, Luo YJ. The impact of perceptual load on the non-conscious processing of fearful faces. PLoS One. 2016:11(5):e0154914. https://doi.org/10.1371/ journal.pone.0154914.
- Whalen PJ, Rauch SL, Etcoff NL, McInerney SC, Lee MB, Jenike MA. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. J Neurosci. 1998:18(1):411–418. https://doi.org/10.1523/JNEUROSCI.18-01-00411.1998.
- Wickens TD. Elementary signal detection theory. Oxford: Oxford University Press; 2001.
- Widmann A, Schröger E, Maess B. Digital filter design for electrophysiological data—a practical approach. J Neurosci Methods. 2015:250:34–46. https://doi.org/10.1016/j.jneumeth.2014. 08.002.
- Wiens S. Current concerns in visual masking. *Emotion*. 2006:6(4):675. https://doi.org/10.1037/1528-3542.6.4.675.
- Willenbockel V, Sadr J, Fiset D, Horne GO, Gosselin F, Tanaka JW. Controlling low-level image properties: the SHINE toolbox. Behav Res Methods. 2010:42(3):671–684. https://doi.org/10.3758/ BRM.42.3.671.
- Williams LM, Brown KJ, Das P, Boucsein W, Sokolov EN, Brammer MJ, Gordon E. The dynamics of cortico-amygdala and autonomic activity over the experimental time course of fear perception. Cogn Brain Res. 2004a:21(1):114–123. https://doi.org/10.1016/ j.cogbrainres.2004.06.005.
- Williams LM, Liddell BJ, Rathjen J, Brown KJ, Gray J, Phillips M, Gordon E. Mapping the time course of nonconscious and conscious perception of fear: an integration of central and peripheral measures. *Hum Brain Mapp*. 2004b:21(2):64–74. https://doi.org/10.1002/ hbm.10154.
- Williams MA, Morris AP, McGlone F, Abbott DF, Mattingley JB. Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. J Neurosci. 2004c: 24(12):2898–2904. https://doi.org/10.1523/JNEUROSCI.4977-03. 2004.
- Williams LM, Liddell BJ, Kemp AH, Bryant RA, Meares RA, Peduto AS, Gordon E. Amygdala–prefrontal dissociation of subliminal and supraliminal fear. Hum Brain Mapp. 2006:27(8):652–661. https:// doi.org/10.1002/hbm.20208.
- Wójcik MJ, Nowicka MM, Bola M, Nowicka A. Unconscious detection of one's own image. Psychol Sci. 2019:30(4):471–480. https://doi. org/10.1177/0956797618822971.
- Woodman GF, Luck SJ. Serial deployment of attention during visual search. J Exp Psychol Hum Percept Perform. 2003:29(1):121. https:// doi.org/10.1037/0096-1523.29.1.121.

- Wyart V, Dehaene S, Tallon-Baudry C. Early dissociation between neural signatures of endogenous spatial attention and perceptual awareness during visual masking. Front Hum Neurosci. 2012:6:16. https://doi.org/10.3389/fnhum.2012.00016.
- Yang E, Zald DH, Blake R. Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*. 2007:7(4):882. https://doi.org/10.1037/1528-3542.7.4.882.
- Yokoyama T, Noguchi Y, Kita S. Unconscious processing of direct gaze: evidence from an ERP study. Neuropsychologia. 2013:51(7): 1161–1168. https://doi.org/10.1016/j.neuropsychologia.2013.04. 002.
- Zald DH. The human amygdala and the emotional evaluation of sensory stimuli. Brain Res Rev. 2003:41(1):88–123. https://doi. org/10.1016/S0165-0173(02)00248-5.

Publication 3

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CO-AUTHOR'S STATEMENT

As the first author of the article:

Doradzińska, Ł., & Bola, M. (in press). Early electrophysiological correlates of perceptual consciousness are affected by both exogenous and endogenous attention. *Journal of Cognitive Neuroscience*

I declare that my contribution to this publication included:

- participation in the development of the research concept
- critical analysis of existing literature
- preparation of PYTHON scripts used for data analysis
- electrophysiological data analysis with the extraction of ERP amplitudes
- selection of statistical tools suitable for data analysis
- preparation of R scripts used for statistical analysis
- statistical analysis of ERP amplitudes employing Bayesian mixed models
- analysis of behavioral data employing Bayesian mixed models
- interpretation and discussion of obtained results
- preparation of the initial version of the manuscript
- preparation of all of the figures included in the publication
- participation in correcting and complementing the final version of the manuscript

Depoluinisha

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CO-AUTHOR'S STATEMENT

As a supervisor of Ms. Łucja Doradzińska and a co-author of the article:

Doradzińska, Ł., & Bola, M. (in press). Early electrophysiological correlates of perceptual consciousness are affected by both exogenous and endogenous attention. *Journal of Cognitive Neuroscience*.

I declare that this publication was prepared as a part of OPUS NCN grants I managed (2018/29/B/HS6/02152 and 2019/33/B/HS6/02233). My contribution to the publication included establishing the research concept, substantive supervision, consulting the experimental procedure and the interpretation of obtained results, and correcting the final version of the manuscript.

Decision Letter (JOCN-2023-0259.R3)

- From: h.a.slagter@vu.nl
 - To: I.doradzinska@nencki.edu.pl
 - CC: postle@wisc.edu, CharlotteSmylieJOCN@gmail.com, jcogneuro@gmail.com

Subject: JOCN Manuscript JOCN-2023-0259.R3

Body: 13-Mar-2024

Dear Dr. Doradzińska:

Thank you for submitting your revised manuscript entitled, " Early electrophysiological correlates of perceptual consciousness are affected by both exogenous and endogenous attention" to the Journal of Cognitive Neuroscience.

Upon reading of your comments and the revised manuscript, and based on the favorable comments of the original referees, we are pleased to inform you that we have accepted it for publication in JOCN.

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Early Electrophysiological Correlates of Perceptual Consciousness Are Affected by Both Exogenous and Endogenous Attention

Łucja Doradzińska¹ and Michał Bola²

Abstract

■ It has been proposed that visual awareness negativity (VAN), which is an early ERP component, constitutes a neural correlate of visual consciousness that is independent of perceptual and cognitive mechanisms. In the present study, we investigated whether VAN is indeed a specific marker of phenomenal awareness or rather reflects the involvement of attention. To this end, we reanalyzed data collected in a previously published EEG experiment in which awareness of visual stimuli and two aspects that define attentional involvement, namely, the inherent saliency and task relevance of a stimulus, were manipulated orthogonally. During the experimental procedure, participants (n = 41) were presented with images of faces that were backward-masked or unmasked, fearful or neutral, and defined as task-relevant targets or task-irrelevant distractors. Single-trial

ERP analysis revealed that VAN was highly dependent on attentional manipulations in the early time window (140–200 msec), up to the point that the effect of awareness was not observed for attentionally irrelevant stimuli (i.e., neutral faces presented as distractors). In the late time window (200–350 msec), VAN was present in all attentional conditions, but its amplitude was significantly higher in response to fearful faces and taskrelevant face images than in response to neutral ones and task-irrelevant ones, respectively. In conclusion, we demonstrate that the amplitude of VAN is highly dependent on both exogenous (stimulus saliency) and endogenous attention (task requirements). Our results challenge the view that VAN constitutes an attention-independent correlate of phenomenal awareness. ■

INTRODUCTION

Identifying proper neural correlates of consciousness (NCC) requires specifying a neural event that is both necessary and sufficient for the occurrence of a given conscious percept (Crick & Koch, 2003). Although multiple mechanisms have been proposed to constitute NCC (review: Koch, Massimini, Boly, & Tononi, 2016), the activity of the modality-specific sensory cortices that occurs shortly after a stimulus is currently considered the most plausible correlate of perceptual awareness (review: Dembski, Koch, & Pitts, 2021; Förster, Koivisto, & Revonsuo, 2020). Evidence supporting this view comes predominantly from studies that compared electrophysiological activity evoked by conscious and unconscious stimuli, revealing that conscious perception is related to more negative values of ERPs within the first 150–350 msec of stimulus processing (Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo, 2016; Koivisto & Revonsuo, 2010; Ojanen, Revonsuo, & Sams, 2003). Such a negative awareness-related ERP component was initially observed in the visual modality and was thus termed visual

awareness negativity (VAN; Koivisto & Revonsuo, 2010). Importantly, contrasting perceived and unperceived stimuli in the auditory (Schlossmacher, Dellert, Bruchmann, & Straube, 2021; Eklund & Wiens, 2019; Dykstra, Halgren, Gutschalk, Eskandar, & Cash, 2016; Gutschalk, Micheyl, & Oxenham, 2008) and tactile modalities (Schröder, Nierhaus, & Blankenburg, 2021; Auksztulewicz & Blankenburg, 2013; Auksztulewicz, Spitzer, & Blankenburg, 2012) yielded similar early negative components, albeit occurring in the respective modality-specific brain regions. Therefore, based on the assumption that all the observed components reflect the general neural mechanism of perceptual consciousness, the umbrella term "perceptual awareness negativity" (PAN) has been proposed (Dembski et al., 2021). What further supports PAN as a specific marker of phenomenal awareness is a linear dependency between the subjective ratings of awareness and PAN amplitude (Eiserbeck, Enge, Rabovsky, & Abdel Rahman, 2022; Derda et al., 2019; Andersen, Pedersen, Sandberg, & Overgaard, 2016; Koivisto & Grassini, 2016; Auksztulewicz & Blankenburg, 2013), as well as the fact that PAN has been observed in response to consciously perceived stimuli, irrespective of the type of task performed (Andersen, Vinding, Sandberg, & Overgaard, 2022; Eklund, Gerdfeldter, & Wiens, 2019,

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2020; Eklund & Wiens, 2018; Koivisto & Grassini, 2016; Pitts, Metzler et al., 2014) and even when the stimulus was irrelevant to the task (i.e., in a no-report paradigm; Sun, Zeng, Chen, Zhao, & Fu, 2023; Kronemer et al., 2022; Dellert et al., 2021; Schlossmacher, Dellert, Bruchmann, & Straube, 2021; Schlossmacher, Dellert, Pitts, Bruchmann, & Straube, 2020; Shafto & Pitts, 2015; Pitts, Martínez, & Hillyard, 2012). PAN is assumed to reflect the activity of local feedback projections in the modality-specific sensory cortex (Förster et al., 2020); therefore, it is typically interpreted in relation to 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).

However, establishing that a given process is a proper NCC requires demonstrating that it is not reflecting other co-occurring perceptual or cognitive mechanisms (Aru, Bachmann, Singer, & Melloni, 2012; de Graaf, Hsieh, & Sack, 2012). One mechanism that is closely related to perceptual awareness and might constitute an important confound, particularly at the early processing stages, is selective attention (Maier & Tsuchiya, 2021; Koch & Tsuchiya, 2007). Although RPT assumes that local recurrent activity in sensory regions is isolated from the influence of attentional and cognitive processes (which, according to RPT, involve activity of frontoparietal networks; Lamme, 2003), multiple neurophysiological studies conducted in animal models (Buffalo, Fries, Landman, Liang, & Desimone, 2010; Noudoost, Chang, Steinmetz, & Moore, 2010; Fries, Womelsdorf, Oostenveld, & Desimone, 2008; Reynolds & Chelazzi, 2004; Maunsell & Cook, 2002; Luck, Girelli, McDermott, & Ford, 1997; Desimone & Duncan, 1995) and human participants (Pessoa, Kastner, & Ungerleider, 2003; Kastner & Ungerleider, 2001; Luck, Woodman, & Vogel, 2000; Heinze et al., 1994; Hillyard, 1993; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; for review see: Moore & Zirnsak, 2017; Womelsdorf & Fries, 2007) have challenged this claim by showing that local feedback connections play an essential role in the neural mechanism of selective attention. In line with these findings, negative differential ERP components that are very similar to VAN in terms of timing and topography have been identified and investigated as markers of attentional amplification of visual stimuli in human ERP studies (review: Luck, 2012; Luck & Kappenman, 2012). For instance, selection negativity is an early negative deflection found when the ERP waveform evoked by stimuli characterized by task-relevant features is compared with ERP evoked by irrelevant ones (Mado Proverbio & Zani, 2003; Hillyard & Anllo-Vento, 1998; Harter & Aine, 1984). Furthermore, early posterior negativity is a similar early component that differentiates neural response to emotional stimuli from neural activity evoked by neutral ones (Langeslag & van Strien, 2018; Schupp, Junghöfer, Weike, & Hamm, 2004; Junghöfer, Bradley, Elbert, & Lang, 2001). Finally, the N2 posterior contralateral component

(N2pc) is a waveform that is more negative in the hemisphere that is processing the salient stimulus than in the hemisphere that is processing the nonsalient one; therefore, it is considered to indicate spatial attention shifts (Kappenman, Farrens, Luck, & Proudfit, 2014; Eimer, 1996; Luck & Hillyard, 1994). The only aspect distinguishing these attention-related components from VAN is the baseline against which the negative deflection is established: Whereas VAN is calculated against ERP activity evoked by unconscious (subliminal) stimuli, the baseline for the attention-related components is the ERP response to attentionally irrelevant stimuli. Thus, the literature regarding attentional processing indicates that the early neurophysiological markers of attention might be very similar to the proposed early markers of perceptual awareness (see: Bola & Doradzińska, 2021).

Previous work aiming to dissociate the early ERP correlates of awareness and feature-based attention within one experimental procedure provided inconclusive results. A robust body of evidence collected by studies using the inattentional blindness paradigm indicates that ERP amplitude in the VAN time window can be affected by the task relevance of perceived stimuli (Sun et al., 2023; Dellert et al., 2021; Schlossmacher et al., 2020; Schelonka, Graulty, Canseco-Gonzalez, & Pitts, 2017; Shafto & Pitts, 2015; Pitts et al., 2012; for a review, see Hutchinson, 2019). However, the inattentional blindness paradigm does not allow for conclusions about the modulation of the amplitude of VAN, understood as the difference between seen and unseen stimuli, as it lacks the taskrelevant unconscious condition. Some studies that did include an orthogonal manipulation of awareness and relevance, thus testing the interaction between VAN and attention, found that this component is not modulated by attention-related factors, thus concluding that it constitutes a specific index of phenomenal awareness (Dellert et al., 2022; Koivisto et al., 2008; Koivisto & Revonsuo, 2007). Yet, other studies using a similar design have challenged this conclusion by showing that the amplitude of VAN can be influenced by task requirements or the relevance of perceived stimuli (Andersen et al., 2022; Zotto & Pegna, 2015; Pitts, Metzler et al., 2014; Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2008; Koivisto, Revonsuo, & Lehtonen, 2006; Koivisto, Revonsuo, & Salminen, 2005). Moreover, clearly visible stimuli presented on the unattended side of the visual field did not evoke VAN in a study by Koivisto, Kainulainen, and Revonsuo (2009), which suggests that VAN might not be necessary for perceptual awareness. Relatedly, VAN might also not be sufficient for awareness, as VAN-like negativity has been observed in response to subliminal stimuli that are intrinsically salient or assigned as task-relevant (Bola, Paź, Doradzińska, & Nowicka, 2021; Travis, Dux, & Mattingley, 2019; Koivisto & Grassini, 2016; Axelrod, Bar, & Rees, 2015; Koivisto & Revonsuo, 2007, 2008; review: Mudrik & Deouell, 2022). Thus, the relation between selective attention, perceptual awareness,

and VAN remains a matter of ongoing debate (Bola & Doradzińska, 2021).

In the present work, we aimed to systematically examine the impact of various attentional manipulations on VAN. To this end, we reanalyzed data collected in our previous experiment (Doradzińska & Bola, 2023), in which participants were presented with images of faces while exogenous attention (defined as stimulus intrinsic saliency), endogenous attention (defined as task relevance), and stimulus visibility were manipulated orthogonally. Stimulus saliency was determined by the emotional expression of faces, which could be either fearful (salient) or neutral (nonsalient). During the experiment, faces were combined in pairs and presented bilaterally on the screen; this made it possible to investigate, first, the general attentional prioritization effect, obtained by contrasting ERP responses to trials containing a pair of fearful faces against trials containing a pair of neutral ones; second, shifts of spatial attention, indicated by the lateralization of ERP effects in trials in which a fearful face was displayed on one side of the screen, accompanied by a neutral face on the opposite side. Task relevance was defined by two tasks included in the procedure: In one, faces were defined as targets; in the other, they were defined as task-irrelevant distractors. To manipulate the visibility, these face images were displayed briefly, followed by a backward mask in the unconscious condition. This experimental design allowed us to examine, within one statistical model, how VAN-like activity is related to awareness, spatial and nonspatial attentional effects evoked by stimulus saliency, and task relevance. Moreover, although the time window of VAN is often described as overlapping with N1 and N2 components (Förster et al., 2020), some previous studies have distinguished both an early part of VAN that overlaps with the N1 component, and a late part of VAN that overlaps with the P2 and N2 components, thus suggesting that these two subcomponents might exhibit different relations with selective attention (Railo, Koivisto, & Revonsuo, 2011; Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2007, 2008; Koivisto, Revonsuo, & Salminen, 2005). On the basis of these findings, in the present study, we also defined the early and late VAN time windows separately. To maximize the sensitivity of the conducted analyses, we applied a single-trial approach and fitted Bayesian hierarchical models to the collected data.

In line with the existing body of evidence, we expected to observe the general effect of stimulus awareness in the form of VAN. Specifically, we predicted that unmasked, visible stimuli would evoke lower ERP waveform values in both the early and late VAN time windows than ERPs recorded in the masked condition. Regarding the impact of exogenous and endogenous attention, we hypothesized that absolute ERP values would be modulated by both stimulus saliency and task relevance in VAN time windows. In terms of stimulus saliency, we expected to see both the effect of general attentional prioritization, defined as more negative ERP values in response to trials containing two fearful faces, as well as the lateralization of ERP response in the form of N2pc indexing spatial attention shifts toward a fearful face (when combined with a neutral face on the opposite side of the screen).

The main goal of our analysis was to investigate the interaction between awareness and attention. We expected to obtain one of three possible outcomes. The first scenario assumed that stimulus visibility would not interact with saliency and task relevance, which would indicate that the analyzed early ERP response reflects attention and awareness in an additive manner; thus, these two processes can be easily separated on the neural level. The second possibility was that awareness and attention would interact, specifically that VAN evoked by nonsalient and task-irrelevant stimuli would be attenuated when compared with salient and task-relevant ones, respectively. This would suggest a nonadditive nature of neural activity related to awareness and attention, thus challenging VAN as a pure and specific NCC. Third, based on previous results (Koivisto et al., 2009), we also considered the possibility that stimuli that do not engage either type of attention (i.e., stimuli that are neither salient nor task-relevant) might not evoke VAN at all. This would provide even stronger evidence against VAN as a genuine NCC. Finally, in line with the view that mechanisms related to awareness emerge before attentional involvement, we considered that the modulation of VAN by attention might be present only in the late time window, and thus that VAN can be distinguished from attention-related ERP effects on the basis of its earlier temporal profile (Koivisto & Revonsuo, 2010).

In addition, we also conducted an analysis of the P3b component, which is proposed to reflect a putative late mechanism of conscious access (Dehaene & Changeux, 2011). However, multiple studies have already found that P3b is closely related to task relevance rather than perceptual awareness of a stimulus (Dellert, Krebs et al., 2022; Kronemer et al., 2022; Dellert, Müller-Bardorff et al., 2021; Schlossmacher et al., 2021; Schröder et al., 2021; Sergent et al., 2016; Pitts, Metzler, et al., 2014; Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014). We thus hypothesized that in our study, we would also observe a decrease and perhaps even a complete suppression of awareness-related effects on P3b amplitude in the task-irrelevant condition.

METHODS

Participants

In the present study, we reanalyzed an already published data set, which comprised EEG recordings from 41 adult participants (20 females, mean age = 26.9 years, standard deviation = 5.1 years, range: 18–40 years, one left-handed) and was originally collected to investigate EEG markers of unconscious attentional bias toward threats (Doradzińska & Bola, 2023). The sample size was determined based on

the estimated size of the unconscious attentional reaction to threats. All of the collected data sets were included in the present analysis. Participants declared normal or corrected-to-normal vision and no history of mental or neurological disorders. Before the experiment, they provided written informed consent and were compensated for their time (150 PLN = ca. 33 EUR). The experimental procedures used in this study were approved by the Research Ethics Committee at Nicolaus Copernicus University (KB 447/2020).

Stimuli

The visual stimuli presented in our study were photographs of eight female and eight male Caucasian models selected from the NimStim set of facial expressions (Tottenham et al., 2009).¹ For each model, we selected two pictures: one with a neutral and one with a fearful expression. Importantly, to obtain the highest distinctiveness of the presented emotions, we used only images of fearful faces with open mouths and images of neutral faces with closed mouths. The photographs were aligned and scaled to ensure that the on-screen position of significant face elements (eyes, nose, and mouth) was consistent across images; the images were then cropped in an oval shape (i.e., without hair). Stimuli were converted to grayscale and normalized in terms of luminance and contrast using the *lumMatch* function from the SHINE toolbox (Willenbockel et al., 2010).

Images of neutral faces were used to create a set of 16 "masks," which were used to backward-mask face stimuli. Fearful faces were not used because the significant components of fearful expressions could influence the visibility of face images presented before masks. Masks were created in GIMP software by manually selecting and copying rectangular pieces from the original images and relocating them (similar to our previous work: Bola et al., 2021; Wójcik, Nowicka, Bola, & Nowicka, 2019). The masks' low-level visual features (e.g., luminance and contrast) were matched to the set of intact face images using the *lumMatcb* SHINE function (Willenbockel et al., 2010).

Procedure

The experimental procedure was programmed using Presentation software (Version 20.1, Neurobehavioral Systems, Inc., www.neurobs.com) and presented on an LCD monitor DELL AW2518HF (24.5 in.) with 1920 \times 1080 resolution (89.91 ppi) and 120-Hz refresh rate. A viewing distance of 60 cm was maintained by an adjustable chinrest. During the experiment, participants were seated in a dimly lit and sound-attenuated room.

The experimental procedure was presented against a gray background (red, green, blue [128, 128, 128]; Figure 1). A white fixation cross (Arial, 48 pt. font size, 0.8×0.8 cm actual size, $0.8^{\circ} \times 0.8^{\circ}$ of visual angle) was displayed in the center of the screen for the entire duration, except for breaks and instruction presentation. Each



Figure 1. (A) Schematic presentation of an experimental trial. (B) The estimated percentage of "neutral" responses obtained in ID tasks, depending on the masking condition, emotional expression of the target face, and the emotional expression of the second face in the pair. Dots depict estimated values; error bars depict 95% CIs derived from the statistical model.
trial started with a 16.7-msec presentation of two oval faces. Face images were scaled to a size of 6.95 cm \times 10.15 cm ($6.6^{\circ} \times 9.6^{\circ}$ of visual angle) and displayed on opposite sides of the screen, with their inner edges at a distance of 4.13 cm (3.9° of visual angle) from the fixation cross. Facial stimuli were combined in four possible ways: two fearful faces; fearful on the left and neutral on the right; fearful on the right and neutral on the left; or two neutral faces. Each combination appeared equally frequently during the procedure. Furthermore, in half of the trials, the faces were immediately followed by a pair of masks (masked condition), displayed for 50 msec and covering the exact area of face presentation; in the other half of trials, faces were followed by an empty screen (unmasked condition). Faces and masks always came from four different yet gender-matched models. Finally, 500 msec after the masks, a pair of white asterisks (Arial, 60 pt. font size, actual size of 0.68×0.64 cm) were displayed on either the left or the right side of the screen, in the same location as the center of one of the previously displayed faces (distance of 7.06 cm from the center of the screen, 6.7° of visual angle). The asterisks were arranged either vertically or horizontally, with a 1.70-cm distance between them $(1.6^{\circ} \text{ of visual angle})$, and they remained on the screen for 150 msec. The trial ended with the participant's response, or 5 sec after the presentation of the asterisks.

The experiment was divided into two blocks: Participants performed a dot-probe (DP) task in one block and an ID task in the other block. In the DP task, participants had to indicate the orientation of the presented asterisks (i.e., vertical or horizontal); therefore, the faces were taskirrelevant. In the ID task, participants were asked to report the expression of the face presented on the same side as the following pair of asterisks (thus, the faces were taskrelevant targets). Participants provided their responses with a button press using their left and right forefingers. The order of tasks and response mapping in both the DP task and the ID task was counterbalanced across participants.

The procedure consisted of 1152 trials in total, 576 per task. Trials were presented in sequences of 32, with random trial-to-trial intervals of 1–2 sec. Each sequence was followed by a self-paced break. Each combination of the following factors was presented exactly once within each sequence in random order: gender of faces, the emotional expression of each face, masking condition, the side of the screen on which the asterisks were presented, and the orientation of the asterisks.

Behavioral Analysis

In the original study (Doradzińska & Bola, 2023), behavioral data from the identification task were analyzed within the signal-detection theory framework (Wickens, 2001). Specifically, the d' and c parameters were calculated for masked and unmasked trials separately, and the obtained values were statistically tested against 0. The d' sensitivity measure expresses the ability of participants to discriminate between two types of stimuli (i.e., fearful and neutral faces). A d' of 0 indicates chance-level performance. Criterion (c) reflects a response bias toward one category of stimuli: In our study, negative c values indicate a bias toward "fearful" responses, whereas positive c values indicate a bias toward "neutral" responses. The obtained results revealed that d' was very low in the masked condition, but it was significantly higher than 0 (M = 0.10, SD =0.18, range = [-0.25, 0.50]), which suggests that participants were able to identify masked stimuli slightly above the chance level. In the unmasked condition, d' values were much higher and also significantly greater than 0 (M = 1.49, SD = 0.47, range = [0.07, 2.56]), which means that when faces were not followed by masks, participants were much better at discriminating emotional expressions. At the same time, c values were significantly higher than 0 in the masked (M = 0.32, SD = 0.41, range = [-0.85, 1.73]) but not in the unmasked condition (M = -0.04, SD = 0.25, range = [-0.97, 0.28]), which suggests that participants presented a bias toward neutral responses when stimuli were followed by masks.

In the present study, we wanted to investigate the impact of the second face displayed on the screen on the responses to the target face (the one followed by the asterisks) in the identification task. For this purpose, we used a Bayesian mixed model to analyze the number of neutral responses in each condition (fearful and neutral faces, masked and unmasked), taking into account the expression of the second face presented in the trial. Thus, from the raw behavioral data, we removed trials in which participants responded before the asterisks were presented or in which no response was made. The rest of the trials (median = 1147, range = [1019, 1152] per participant) were assembled in a long array and entered into the statistical analysis.

In addition, we conducted a frequentist analysis of the influence of the second face on d' and the *c* parameter; this analysis can be found in Appendix A.

EEG Recording and Analysis

In the present analysis, we used EEG recordings that had already been cleaned of artifacts and segmented into epochs for the previous study (Doradzińska & Bola, 2023). The number of epochs in the analyzed data sets was, on average, 1043.88 out of 1152 (range = [653, 1143]). Below, we describe all the details of the data collection and preprocessing steps conducted on the data sets.

The recording of the continuous EEG signal was conducted with 64 Ag/AgCl electrically shielded electrodes (BioSemi Active-electrodes) mounted on an elastic cap (Biosemi) and positioned according to the extended 10–20 system, two reference electrodes (Flat-Type Active-electrodes, BioSemi) located on the left and right earlobes, and four bipolar electrodes (Flat-Type Activeelectrodes, BioSemi) placed at the supra- and sub-orbit of the right eye and at the external canthi. The raw signal was acquired in a Biosemi "zero-ref" setup using a common mode sense active electrode on the left and a driven right leg passive electrode placed in the elastic cap between the Pz and POz channels on the right side. The signal registered by the bipolar electrodes was offline transformed into a VEOG and a HEOG. The offset values of active electrodes were kept between -10 and 10 mV. The raw, unreferenced signal was amplified and digitized at a sampling rate of 2048 Hz by an ActiveTwo AD-box (BioSemi).

Offline analysis of the EEG and EOG signals was performed using the MNE 0.24.1 package (Gramfort et al., 2013, 2014) for Python 3.7. The continuous EEG signal was first preprocessed, including rereferencing it to the mean signal recorded on the right and left earlobes and band-pass filtering from 0.1 to 40 Hz (-6-dB cutoff) with a zero-phase finite impulse response filter with a Hamming window (*filter(*) method of *Raw* object in the MNE package; Widmann, Schröger, & Maess, 2015). After these steps, the signal was segmented into 1400 msec-long epochs, from -200 to 1200 msec with respect to the face image onset. Furthermore, on each channel, we applied a baseline correction against the mean voltage during the 200-msec prestimulus period and then resampled the signal to 256 Hz. Finally, a few more steps were performed to remove faulty trials and clean the signal of movement artifacts. Removing no-response trials and trials in which a button press preceded the onset of asterisks reduced the total number of trials by a median of five trials (range = [0, 125]) out of 1152. Next, epochs with HEOG maximum peak-to-peak signal amplitude exceeding 80 µV in the 0- to 500-msec time window, or with VEOG maximum peakto-peak signal amplitude exceeding 140 μ V in the -100to 100-msec time window were removed to exclude trials in which participants blinked during the presentation of the stimulus or moved their eyes to one of the faces in the time window chosen for ERP analysis. The remaining oculomotor artifacts were identified by decomposing the EEG signal into 64 independent components using independent component analysis (Makeig, Jung, Ghahremani, & Sejnowski, 1996), and each component was correlated with the HEOG and VEOG channels (using Pearson correlation). Iterative z-scoring allowed us to select components whose correlation coefficients exceeded 3 SDs from the mean, which were then excluded from the data (find bad eogs() method of independent component analysis object in the MNE package). In the last step, we applied a standardized and automatic artifact rejection procedure implemented in the Autoreject package (Jas, Engemann, Bekhti, Raimondo, & Gramfort, 2017; Jas, Engemann, Raimondo, Bekhti, & Gramfort, 2016). The algorithm first calculated the rejection thresholds individually for each participant and channel (*fit(*) method of the AutoReject object in the Autoreject package; we choose a random search method); then, it removed single-channel

signal fragments that exceeded the threshold and filled the resulting gaps by interpolating the signal from the neighboring electrodes. If too many bad channels were discovered in a given epoch, the whole segment was rejected from the data set (*transform(*) method of the *AutoReject* object in the Autoreject package; for details of the procedure, see Jas, Engemann, Bekhti et al., 2017; Jas, Engemann, Raimondo et al., 2016).

ERP Analysis

ERP waveforms used for visualization purposes were obtained by averaging the signal across epochs within each condition. The spatio-temporal window of VAN was specified based on previous studies (for a review see: Dembski et al., 2021; Förster et al., 2020). According to the existing literature, VAN is observed over occipitotemporal scalp regions (Dellert et al., 2021; Dembski et al., 2021; Förster et al., 2020; Shafto & Pitts, 2015; Pitts et al., 2012; Koivisto & Revonsuo, 2010); therefore, the P7, P8, PO7, PO8, P9, P10 cluster of electrodes was chosen for the analysis. As some previous studies have reported, VAN can also be observed on midline occipital electrodes (e.g., Koivisto & Grassini, 2016; Koivisto et al., 2009; Koivisto & Revonsuo, 2007, 2008); therefore, an additional control analysis of the cluster containing PO3, POz, PO4, O1, Oz, and O2 was conducted, which can be found in Appendix C. To reduce the probability of Type I errors, the temporal windows were defined orthogonally to the statistical comparisons conducted between conditions (Keil et al., 2014). Specifically, we created grand-averaged waveforms by pooling the signals recorded from the chosen electrodes (Figure 2); on the basis of a visual inspection, we selected the 140- to 200-msec window for the early VAN (N170 component) and the 200- to 350-msec window for the late VAN (P2-N2 components). The time window for the analysis of the P3b component was the same as in the original study (Doradzińska & Bola, 2023).

ERP effects were analyzed using hierarchical Bayesian models. In the analysis of early VAN, late VAN, and P3 components, we investigated the effects of masking, task relevance, and the effect of emotional content presented on the screen (fearful vs. neutral expressions). Therefore, the analysis was performed on data collected from trials containing either two neutral or two emotional faces. For each component, we calculated the mean EEG signal amplitude, pooled from the predefined electrodes in a given time window. This was done for each epoch separately, and the values obtained for all participants were pooled together in three arrays (one for each component), each consisting of 21,359 data points that entered the statistical analysis.

Furthermore, we conducted an analysis of the impact on early and late VAN of the spatial attention reaction to fearful faces presented on one side of the visual field. In this case, only trials containing one neutral face and one fearful face were used. The models used in this analysis



Figure 2. ERPs time-locked to the onset of face images. The left column depicts ERP waveforms averaged over the P7, P8, P07, P08, P9, and P10 electrodes; the right column depicts waveforms averaged over CP1, CP2, CP2, P1, P2, and P2. The schematic drawing of the head near each column depicts the locations of the channels that were averaged to obtain the ERP waveform. Time windows used for analysis of early and late VAN are highlighted on the left column in light and dark gray, respectively. The time window chosen for analysis of the P3b component is highlighted in gray on the right column.

contained factors of masking, task relevance, and the side on which the activity was measured in relation to the side on which the fearful face was presented (contra- or ipsilateral). For each trial, we calculated the mean amplitudes recorded in a given time window from the ipsilateral and contralateral electrodes, and the obtained values were pooled together across participants. This resulted in two arrays of 42,880 data points each (corresponding to the total number of 21,440 analyzed epochs), representing early and late VAN, which were introduced into the statistical models.

In addition, we conducted a frequentist analysis of the early and late VAN, as well as the lateralized effects in this spatio-temporal window. The description and the results of this analysis can be found in Appendix B.

The *d*['] values obtained in the original study (Doradzińska & Bola, 2023) were significantly higher than zero in the masked condition, suggesting better than random performance in the ID task. To exclude the potential confounding influence of performance on ERP effects, we performed an additional analysis of late and early VAN recorded over the posterior temporal cluster, in which we compared the ERP values obtained from the trials in which participants gave correct and incorrect responses. The description of this analysis and the results can be found in Appendix D.

Statistical Analysis

All behavioral and ERP effects were statistically evaluated using Bayesian mixed models. The analysis was conducted in RStudio 1.4.1717 (RStudio Team, 2021), which is opensource software based on the R programming language (R Core Team, 2021). Models were fitted using the "brms" package (Bürkner, 2017). For each analysis, to establish a maximal fixed-effect structure that is well suited to our

data, we conducted an iterative reduction of model complexity, starting with the model that contained all considered population-level factors and their interactions, and ending with the simple intercept model, with the random-effect structure fixed across all models in the analvsis. The selection of priors for population-level coefficients was based on the recommendations provided by the developers of Stan (Stan Development Team, 2024). In Gaussian models, we applied normal distribution priors with mean = 0 and standard deviation = 10 times sigma, that is, a dispersion parameter derived from the intercept model. In Bernulli models, normal distribution priors with mean 0 and standard deviation equal to 10 were used. In both cases, selected priors can be categorized as weakly informative. Model convergence was verified by checking whether R parameters for all effects were equal to 1; only models that successfully converged were considered for further analysis. The obtained models were evaluated using Pareto smoothed importance-sampling leave-oneout cross-validation, implemented in the "loo" package (Vehtari, Gelman, & Gabry, 2017); the final model was selected based on the ELPD (Expected Log Pointwise Predictive Density for a new observation) and the standard error of the estimated ELPD difference between the evaluated model and the best one. Specifically, we choose the most complex model for which the ELPD distance from the best model did not exceed 2 SEs. All models selected during this procedure and described in the Results section contain the considered population-level effects and all possible interactions between them.

Behavioral responses were analyzed using the Bernoulli model with a probit link function and a random intercept of participant. Population-level effects included three 2level factors of *target* (fearful or neutral emotion expressed by the face that participants had to identify in a given trial), *masking* (masked or unmasked), and *sec-ond face* (emotional expression of a face displayed with the target on the opposite side of the screen; fearful or neutral), and their interactions.

ERP effects were investigated using linear Gaussian models with the identity link function. Before the analysis of each component, trials in which ERP amplitude exceeded 3 SDs from the mean were excluded from the data set (less than 0.9% of datapoints). Models used for all analyses contained a random effect structure, which included a random intercept of participants and random slopes of all considered population-level effects and their interactions. Fixed effects in the analysis of nonlateralized ERP effects (early and late VAN, and P3 component) included three 2-level factors: masking (masked or unmasked condition), emotion (fearful or neutral), and task relevance (task-relevant or task-irrelevant condition; trials from the ID or DP tasks, respectively), and their interactions. The analyses, which accounted for the lateralized effect of spatial attention reaction to the emotional face presented on one side of the screen (lateralized early and late VAN), involved fixed factors of masking and task relevance, a two-level side factor (amplitude obtained ipsilaterally or contralaterally with respect to the side of the fearful face presentation), as well as their interactions.

In each analysis, we report estimates (M) and 95% credibility intervals (CI) derived from the final model. Furthermore, to infer the presence and direction of the effects in our data, we performed nonlinear hypothesis testing. In all analyses, we checked for the presence or absence of an awareness-related effect (negative or positive difference between masked and unmasked conditions), and the interaction of this effect with the emotion (or side in case of lateralized effects) and task relevance factors. Furthermore, we investigated the impact of emotional expressions and task on the absolute values of ERP waveforms. We report the evidence ratio for the one-sided hypotheses regarding the differences between conditions (Evid. *Ratio*₁); in the case of small values (i.e., not exceeding 95% CI), we also report the evidence ratio for the hypothesis that the two considered conditions are equal (Evid. Ratio₀). The evidence ratio for the one-sided hypothesis consists of the posterior probability of the hypothesis and the posterior probability of its alternative (i.e., the one-sided hypothesis in the opposite direction), whereas the evidence ratio calculated for the two-sided (point) hypothesis is an equivalent of a Bayes factor computed via the Savage-Dickey density ratio method.

RESULTS

Behavioral Results

The estimates derived from the analysis of behavioral data are presented in Figure 1. In the unmasked condition, we obtained a clear pattern of results: The second face impacted the probability of a neutral response to fearful faces; specifically, when a target fearful face was accompanied by a neutral face, participants were more likely to respond that the target face was fearful (i.e., give a correct response) than when it was accompanied by a neutral face (second face neutral: M = 16.73%, CI [14.73%, 18.90%]; second face fearful: M = 28.59%, CI [25.97%, 31.40%]; Evid. Ratio₁ > 8000). At the same time, the second face did not influence responses to neutral faces (second face neutral: M = 74.81%, CI [72.17%, 77.38%]; second face fearful: M = 75.85%, CI [73.30%, 78.30%]; Evid. Ratio₁ = 4.60, Evid. Ratio₀ = 272.29). Importantly, this pattern was not found in the masked condition, as in this case the number of neutral responses to neither neutral (second face neutral: M = 64.29%, CI [61.32%, 67.22%]; second face fearful: *M* = 62.11%, CI [59.09%, 65.06%]) nor fearful faces (second face neutral: M = 59.09%, CI [55.98%, 62.18%]; second face fearful: M = 59.88%, CI [56.85%, 62.95%)) was influenced by the emotion expressed by the second face displayed on the screen (target neutral, Evid. $Ratio_1 = 0.05$, Evid. $Ratio_0 = 68.73$; target fearful, Evid. Ratio₁ = 2.73, Evid. Ratio₀ = 365.34). These results indicate that when the visibility of presented stimuli is not disturbed, participants' responses to fearful faces were biased by the expression of the second face presented on the screen. Importantly, this effect vanished when the visibility of faces was suppressed (i.e., in the masked condition).

ERP Results

We first investigate whether VAN is modulated by attention in each of the conducted analyses by estimating effects related to awareness (i.e., involving the masking factor) and interactions between awareness and attention-related factors (emotion or side and task relevance). Next, to test whether a VAN-like effect can be induced by the manipulations of exogenous and endogenous attention alone, we evaluate the influence of emotional expressions and task on the absolute values of ERP waveforms.

The results of the analysis of early and late VAN are depicted in Figure 3. The lateralization of VAN in response to a fearful face presented on one side of the screen and accompanied by a neutral face on the other side is presented in Figure 4. The results obtained for the P3 component are displayed in Figure 5.

Early VAN

The analysis of ERP values in the early time window shows that our data provided substantial evidence that presentation of neutral faces in the task-irrelevant condition did not result in awareness-related negativity (masked, $M = -2.52 \,\mu\text{V}$, CI [$-3.27 \,\mu\text{V}$, $-1.78 \,\mu\text{V}$]; unmasked, $M = -2.63 \,\mu\text{V}$, CI [$-3.36 \,\mu\text{V}$, $-1.89 \,\mu\text{V}$]; Evid. Ratio₁ = 2.06, Evid. Ratio₀ = 210.97). In contrast, we observed VAN in response to fearful faces in the task-irrelevant condition



Figure 3. ERP values recorded in the posterior-temporal cluster of electrodes (P7, P07, P9, P8, P08, 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 column, ERPs obtained in the masked and unmasked conditions are plotted separately; the right column depicts the differential waveforms that resulted from the subtraction of the potentials registered in the masked condition. The time windows used for the statistical analysis of the early and late VAN are highlighted in light and dark gray, respectively. (B) The estimated ERP signal values in the early (left column) and late (right column) VAN time windows with respect to task relevance, masking condition, and emotional expression of presented faces. Dots depict estimated values; error bars depict 95% CIs derived from the statistical model.

(masked, $M = -2.55 \,\mu$ V, CI [-3.30 μ V, -1.80 μ V]; unmasked, $M = -3.17 \,\mu$ V, CI [-3.92 μ V, -2.40 μ V]; Evid. Ratio₁ = 189.48) and to both neutral (masked, $M = -2.65 \,\mu$ V, CI [-3.58 μ V, -1.72 μ V]; unmasked, $M = -3.38 \,\mu$ V, CI [-4.25 μ V, -2.49 μ V]; Evid. Ratio₁ = 295.30) and fearful faces (masked, $M = -2.98 \,\mu$ V, CI [-3.90 μ V, -2.04 μ V]; unmasked, $M = -3.66 \,\mu$ V, CI [-4.56 μ V, -2.76 μ V]; Evid. Ratio₁ = 172.91) in the task-relevant condition. The analysis of interactions between masking and other factors indicated that the emotional expression of faces in the task-relevant condition influenced the amplitude of VAN, resulting in greater values in response to fearful faces (Evid. Ratio₁ = 75.92). However, this interaction was not found in the task-relevant condition (Evid. Ratio₁ = 0.77, Evid. Ratio₀ = 347.68). Furthermore, task relevance increased the amplitude of awareness-related negativity evoked by neutral faces (Evid. Ratio₁ = 227.57), but not by fearful faces (Evid. Ratio₁ = 1.53, Evid. Ratio₀ = 334.25).

The emotion factor influenced ERPs in the taskirrelevant condition: Fearful faces resulted in lower ERP values than neutral faces, but only when stimuli were not masked (masked, Evid. Ratio₁ = 1.32, Evid. Ratio₀ = 369.94; unmasked, Evid. Ratio₁ = 1332.33). Surprisingly, in the task-relevant condition, the effect of emotion was present in the masked condition but absent in the unmasked condition (masked, Evid. $Ratio_1 = 30.87$; unmasked, Evid. $Ratio_1 = 15.39$; Evid. $Ratio_0 = 186.78$). As for the impact of task relevance, task-relevant stimuli evoked overall lower ERP values, but only when stimuli were unmasked (masked neutral, Evid. $Ratio_1 = 2.34$; Evid. $Ratio_0 = 198.87$; masked fearful, Evid. $Ratio_1 = 18.23$; Evid. $Ratio_0 = 84.61$; unmasked neutral, Evid. $Ratio_1 = 33.48$).

Overall, our results indicate that early VAN is gated by attentional engagement and thus can be completely suppressed when stimuli are neither nonsalient nor taskirrelevant. In addition, in the conscious condition, we found that both endogenous and exogenous attention can produce a negative deflection of the ERP waveform that is similar to VAN; moreover, we found that VAN-like negativity can be evoked by unconscious salient stimuli, but only in the task-relevant condition.

Late VAN

Analysis of the late VAN recorded in the posteriortemporal cluster indicated that the effect of masking was present in all experimental conditions, with unmasked



Figure 4. Lateralized ERP values recorded in the posterior-temporal cluster of electrodes (P7, PO7, P9, P8, PO8, and P10) in response to trials with one fearful and one neutral face. (A) ERPs time-locked to the onset of face images. In the left column, ERPs obtained in the masked and unmasked conditions are plotted separately; the right column depicts differential waveforms that resulted from the subtraction of the potentials 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 column) and late (right column) VAN time windows with respect to task relevance, masking condition, and the hemisphere processing the fearful (contra) and neutral (ipsi) face. Dots depict estimated values, and error bars depict 95% CIs derived from the statistical model.



Figure 5. ERP values recorded in the parietal cluster of electrodes (CP1, CP2, CP2, P1, Pz, and P2) in response to trials with two fearful or two neutral faces. (A) ERPs time-locked to the onset of face images. In the left column, ERPs obtained in the masked and unmasked conditions are plotted separately; the right column depicts the differential waveforms that resulted from the subtraction of the potentials registered in the masked condition. The time windows used for the statistical analysis of the P3b component are highlighted in light and dark gray, respectively. (B) The estimated ERP signal values in the P3b time-window with respect to task relevance, masking condition, and emotional expression of presented faces. Dots depict estimated values; error bars depict 95% CIs derived from the statistical model.

stimuli evoking lower ERP values than masked ones (taskirrelevant neutral: masked, $M = 3.44 \ \mu$ V, CI [2.71 μ V, 4.15 μ V], unmasked, $M = 1.83 \ \mu$ V, CI [1.26 μ V, 2.40 μ V], Evid. Ratio₁ > 8000; task-irrelevant fearful: masked, M =3.61 μ V, CI [2.88 μ V, 4.33 μ V], unmasked, $M = 1.54 \ \mu$ V, CI [1.00 μ V, 2.09 μ V], Evid. Ratio₁ > 8000; task-relevant neutral: masked, $M = 2.58 \ \mu$ V, CI [1.70 μ V, 3.47 μ V], unmasked, $M = -0.30 \ \mu$ V, CI [-1.10 μ V, 0.49 μ V] Evid. Ratio₁ > 8000; task-relevant fearful: masked, $M = 1.47 \ \mu$ V, CI [1.56 μ V, 3.37 μ V], unmasked, $M = -0.66 \ \mu$ V, CI [-1.52 μ V, 0.20 μ V], Evid. Ratio₁ > 8000). Analysis of interactions between masking and other factors revealed that VAN was impacted by the emotion factor, with fearful faces evoking greater amplitude of this differential component, but only in the task-irrelevant condition (task-irrelevant, Evid. Ratio₁ = 36.74; task-relevant, Evid. Ratio₁ = 5.02, Evid. Ratio₀ = 212.87). Task relevance, on the other hand, influenced the amplitude of VAN regardless of the faces' emotional expression, meaning that task-relevant stimuli evoked greater VAN when compared with task-irrelevant ones (neutral, Evid. Ratio₁ = 20.39; fearful, Evid. Ratio₁ = 28.41).

In addition, we explored the effect of emotion and task relevance on the absolute ERP values registered in the late VAN time window. We found that fearful faces were associated with lower ERP values in the unmasked condition (task-irrelevant masked, Evid. Ratio₁ = 0.16, Evid. Ratio₀ = 194.30; task-relevant masked, Evid. Ratio₁ = 2.99, Evid. Ratio₀ = 366.31; task-irrelevant unmasked, Evid. Ratio₁ = 20.39; task-relevant unmasked, Evid. Ratio₁ = 28.41). At the same time, task-relevant stimuli evoked lower ERP values than task-irrelevant ones in all masking conditions, and for both emotional expressions (neutral masked, Evid. Ratio₁ = 162.27; fearful masked, Evid. Ratio₁ = 3999.00; neutral unmasked, Evid. Ratio₁ > 8000; fearful unmasked, Evid. Ratio₁ > 8000).

Summarizing, late VAN was present in all experimental conditions, but it was robustly modulated by both endogenous and exogenous attention. The impact of both attentional factors on VAN was interactive, as stimulus saliency modulated the amplitude of VAN in the task-irrelevant condition only. Furthermore, in the conscious condition, we found a VAN-like negative effect produced by both stimulus saliency and task relevance. Importantly, the negative deflection of the ERP signal evoked by task relevance was also present in the unconscious condition.

Lateralization of Early VAN

When contrasting masked and unmasked stimuli in the task-irrelevant condition, our analysis revealed that VAN was present in the hemisphere that was processing a fearful face (contra; masked, $M = -2.67 \,\mu\text{V}$, CI [-3.36 μV , $-1.99 \,\mu\text{V}$; unmasked, $M = -3.06 \,\mu\text{V}$, CI [$-3.79 \,\mu\text{V}$, $-2.36 \,\mu\text{V}$; Evid. Ratio₁ = 40.45) but not in the one processing a neutral face (ipsi; masked, $M = -2.51 \,\mu\text{V}$, CI $[-3.19 \ \mu\text{V}, -1.84 \ \mu\text{V}];$ unmasked, $M = -2.63 \ \mu\text{V},$ CI $[-3.36 \,\mu\text{V}, -1.95 \,\mu\text{V}]$; Evid. Ratio₁ = 2.80, Evid. Ratio₀ = 287.92). In the task-relevant condition, a negative awareness-related effect was observed in both hemispheres (ipsi: masked, $M = -2.66 \mu$ V, CI [-3.54 μ V, $-1.79 \ \mu\text{V}$, unmasked, $M = -3.23 \ \mu\text{V}$, CI [$-4.11 \ \mu\text{V}$, -2.42μ V], Evid. Ratio₁ = 306.69; contra: masked, M = $-2.71 \,\mu\text{V}$, CI [$-3.61 \,\mu\text{V}$, $-1.85 \,\mu\text{V}$], unmasked, M $-3.49 \ \mu\text{V}$, CI [$-4.36 \ \mu\text{V}$, $-2.65 \ \mu\text{V}$], Evid. Ratio₁ = 7999.00). Furthermore, VAN amplitudes in the ipsilateral and contralateral hemisphere were equal for each of the tasks (task-irrelevant, Evid. $Ratio_1 = 12.79$, Evid. $Ratio_0 =$ 123.91; task-relevant, Evid. $Ratio_1 = 6.25$, Evid. $Ratio_0 =$ 274.76), but task relevance influenced VAN in both hemispheres: In the task-relevant condition, this component reached greater amplitudes than in the task-irrelevant one (ipsi, Evid. $Ratio_1 = 54.17$; contra, Evid. $Ratio_1 =$ 26.40).

The effect of side on the absolute values of the ERP waveform was absent in the masked condition (taskirrelevant, Evid. Ratio₁ = 8.07, Evid. Ratio₀ = 243.55; task-relevant, Evid. Ratio₁ = 1.86, Evid. Ratio₀ = 656.29) and present in the unmasked condition, with ERP values recorded contralaterally to the fearful face being lower than those recorded ipsilaterally (task-irrelevant, Evid. Ratio₁ = 999.00; task-relevant, Evid. Ratio₁ = 30.37). Similarly, task relevance impacted ERP values evoked by unmasked faces, with task-relevant stimuli resulting in lower values than task-irrelevant ones (neutral, Evid. Ratio₁ = 319.00; fearful, Evid. Ratio₁ = 37.10), but this effect was absent in the masked condition (neutral, Evid. Ratio₁ = 2.81, Evid. Ratio₀ = 225.81; fearful, Evid. Ratio₁ = 1.32, Evid. Ratio₀ = 387.64).

Therefore, the analysis of lateralized effects on VAN in the early time window indicates that awareness-related negativity was gated primarily by task relevance. Although we found strong evidence in the task-irrelevant condition for the absence of VAN in the hemisphere processing the neutral face, and we found some evidence for the presence of VAN in the hemisphere processing the fearful face, the differences in the amplitudes of VAN between hemispheres were too small to be captured by the model. Furthermore, both exogenous and endogenous attention directed toward visible stimuli were associated with VAN-like negative effects.

Lateralization of the Late VAN

In the late time window, we observed VAN in both hemispheres and both task relevance conditions (task-irrelevant ipsi: masked, $M = 3.27 \,\mu\text{V}$, CI [2.51 μV , 4.03 μV]; unmasked, $M = 1.89 \,\mu\text{V}, \text{CI} [1.25 \,\mu\text{V}, 2.57 \,\mu\text{V}]; \text{Evid. Ratio}_1 > 8000; \text{task-}$ irrelevant contra: masked, $M = 3.36 \mu V$, CI [2.60 μV , 4.12 μ V]; unmasked, $M = 1.44 \mu$ V, CI [0.80 μ V, 2.11 μ V]; Evid. Ratio₁ > 8000; task-relevant ipsi: masked, M =2.53 μ V, CI [1.63 μ V, 3.46 μ V]; unmasked, $M = 0.00 \mu$ V, CI $[-0.88 \,\mu\text{V}, 0.93 \,\mu\text{V}]$; Evid. Ratio₁ > 8000; task-irrelevant contra: masked, $M = 2.64 \,\mu\text{V}$, CI [1.76 μV , 3.53 μV]; unmasked, $M = -0.73 \,\mu\text{V}$, CI [-1.60 μV , 0.21 μV]; Evid. Ratio₁ > 8000). Moreover, our data indicate that the side factor influenced the amplitude of awareness-related negativity in both tasks such that VAN was more pronounced in the hemisphere contralateral to fearful face presentation (task-irrelevant, Evid. Ratio₁ = 570.43; task-relevant, Evid. Ratio₁ > 8000). The effect of masking was also impacted by task relevance, as VAN obtained in the task-relevant condition in both hemispheres exhibited greater amplitudes than in the task-irrelevant condition (ipsi, Evid. Ratio₁ >8000; contra, Evid. Ratio₁ > 8000).

Investigation of absolute ERP values in ipsilateral and contralateral hemispheres revealed that the effect of side was present only in the unmasked condition, with more negative potentials registered in the hemisphere contralateral to the presentation of the fearful face (task-irrelevant masked, Evid. Ratio₁ = 0.30, Evid. Ratio₀ = 383.93 task-relevant; masked, Evid. Ratio₁ = 0.25, Evid. Ratio₀ = 492.94; task-irrelevant unmasked, Evid. Ratio₁ > 8000). In contrast, task relevance impacted ERP values regardless of the mask-ing condition and side. Specifically, task-relevant stimuli evoked overall lower potentials than task-irrelevant ones (ipsi masked, Evid. Ratio₁ = 132.33; contra masked, Evid.

Ratio₁ = 132.33; ipsi unmasked, Evid. Ratio₁ > 8000; contra unmasked, Evid. Ratio₁ > 8000).

In summary, late VAN was present in all conditions, but its amplitude was modulated by both exogenous and endogenous attention. Furthermore, in the conscious condition, both stimulus saliency and task relevance evoked a VAN-like negative effect, whereas such a negative deflection was only induced by task relevance in the unconscious condition.

P3b

Conscious and unconscious stimuli differed in terms of the P3b component amplitude, but only for fearful faces in the task-relevant condition (task-irrelevant neutral: masked, $M = 0.69 \,\mu\text{V}, \,\text{CI} \,[0.06 \,\mu\text{V}, \,1.34 \,\mu\text{V}], \,\text{unmasked}, M =$ $0.20 \,\mu\text{V}$, CI [$-0.40 \,\mu\text{V}$, $0.82 \,\mu\text{V}$], Evid. Ratio₁ = 0.03, Evid. Ratio₀ = 57.21; task-irrelevant fearful: masked, M =0.82 μ V, CI [0.16 μ V, 1.47 μ V], unmasked, $M = 0.11 \mu$ V, CI $[-0.55 \ \mu\text{V}, 0.78 \ \mu\text{V}]$, Evid. Ratio₁ < 0.00125, Evid. Ratio₀ = 16.68; task-relevant neutral: masked, M =4.46 μ V, CI [3.54 μ V, 5.36 μ V], unmasked, $M = 4.34 \mu$ V, CI [3.27 μ V, 5.46 μ V], Evid. Ratio₁ = 0.60, Evid. Ratio₀ = 340.47; task-relevant fearful: masked, $M = 4.45 \,\mu\text{V}$, CI $[3.51 \,\mu\text{V}, 5.41 \,\mu\text{V}]$, unmasked, $M = 6.33 \,\mu\text{V}$, CI $[5.08 \,\mu\text{V}]$, 7.60 μ V], Evid. Ratio₁ > 8000). Unsurprisingly, an analysis of interactions between awareness and other factors revealed that the masking effect was influenced by emotion, with fearful faces resulting in higher positive differences than neutral faces, but only in the task-relevant condition (task-irrelevant, Evid. Ratio₁ = 0.36, Evid. $Ratio_0 = 211.15$; task-relevant, Evid. $Ratio_1 > 8000$). Analogously, task relevance impacted awareness-related differences: The task-relevant condition was associated with higher differential potential, but only in the case of fearful faces (neutral, Evid. Ratio₁ = 4.38, Evid. Ratio₀ = 140.64; fearful, Evid. Ratio₁ > 8000).

As for the absolute values of the P3b component, we obtained results showing that the emotion factor impacted P3b, with task-relevant unmasked fearful faces evoking P3b of higher amplitude than task-relevant unmasked neutral faces (Evid. Ratio₁ > 4.38), but differences between fearful and neutral were absent in other combinations of masking and task relevance (task-irrelevant masked, Evid. Ratio₁ = 2.33, Evid. Ratio₀ = 309.72; task-relevant masked, Evid. Ratio₁ = 1.02, Evid. Ratio₀ = 469.61; task-irrelevant unmasked, Evid. Ratio₁ = 0.58, Evid. $Ratio_0 = 474.04$). On the other hand, task relevance influenced P3b potential in all masking conditions and for all kinds of stimuli (neutral masked, Evid. Ratio₁ > 8000; fearful masked, Evid. Ratio₁ > 8000; neutral unmasked, Evid. Ratio₁ > 8000; fearful unmasked, Evid. Ratio₁ > 8000).

Summarizing, our data provides strong evidence that awareness-related effects on P3b potential are gated by both stimulus saliency and task relevance. Differences between visible and invisible stimuli were observed only in the task-relevant condition and only when the presented faces were salient. Absolute P3b amplitudes were generally higher in the task-relevant condition; when stimuli were visible, they were additionally modulated by their emotional expression.

DISCUSSION

In the present study, we investigated early electrophysiological markers of perceptual awareness and their relation with mechanisms of selective attention. Specifically, we analyzed the impact of attention on VAN, which is a hypothesized marker of phenomenal awareness that is defined as a relatively early (200–300 msec after stimulus onset) negative deflection of the ERP waveform (for reviews see: Dembski et al., 2021; Förster et al., 2020; Rutiku & Bachmann, 2017; Railo et al., 2011; Koivisto & Revonsuo, 2010). Our main finding is that the amplitude of VAN is significantly modulated by both exogenous and endogenous attention, respectively, defined as the intrinsic saliency and task relevance of a presented visual stimulus. In fact, our results indicate that ERP waveforms in both the early (140–200 msec) and late (200–350 msec) time windows of VAN are characterized by a complex intertwining of effects related to awareness and attention, with both processes influencing each other in an interactive, nonlinear manner. Specifically, endogenous attention modulated the amplitude of VAN in both time windows, with task-relevant stimuli resulting in greater VAN amplitudes than task-irrelevant ones. Exogenous attention impacted VAN primarily in the late time window (200-350 msec), with fearful faces evoking more pronounced negativity when compared with neutral ones. Furthermore, the VAN amplitude was higher in the hemisphere contralateral to the presented fearful face-an effect that resembles the N2pc component, which is typically interpreted as a marker of spatial attention shifts. Importantly, in the early time window, the impact of attention was so pronounced that VAN was completely suppressed when presented stimuli were nonsalient and task-irrelevant. Finally, negative VAN-like effects related to both exogenous and endogenous attention were observed in the absence of stimulus awareness. As we hypothesized, the awareness-related effects on the P3b component measured in our study were dependent on the task relevance and saliency of presented stimuli, in line with previous work (Dellert, Krebs et al., 2022; Kronemer et al., 2022; Dellert, Müller-Bardorff et al., 2021; Schlossmacher et al., 2021; Schröder et al., 2021; Sergent et al., 2021; Cohen et al., 2020; Koivisto et al., 2016; Pitts, Metzler, et al., 2014; Pitts, Padwal et al., 2014). Overall, our data suggest that VAN is not a specific marker of consciousness but, at least to a certain extent, it reflects attentional prioritization of a stimulus. Moreover, the neural activity constituting VAN cannot be easily explained as the sum of two overlapping yet separable processes (i.e., awareness and attention).

The Modulation of VAN by Exogenous and Endogenous Attention

Several studies have reported that VAN was not modulated by attention-related factors (Dellert et al., 2022; Koivisto et al., 2008; Koivisto & Revonsuo, 2007). However, this conclusion was based not on confirming that the data indeed supported the null hypothesis (i.e., using the Bayesian approach) but rather on a failure to find a significant interaction between attention and awareness, which, in the case of studies conducted before 2010, can be easily explained by relatively small sample sizes (fewer than 15 participants in each study). In contrast, our analysis was performed on a sample of 41 participants, a size that highly exceeds those previously reported. The recent study by Dellert and colleagues (2022) tested a relatively large sample of participants (n = 38), but, in our opinion, it was characterized by two other caveats. First, an attentional blink paradigm was used, which, by definition, involves the manipulation of awareness via the availability of attentional resources, and therefore the contrast between seen and unseen stimuli might be confounded by the presence or absence of attentional engagement. Second, similarly to previous work, the conclusions of Dellert and colleagues (2022) were also based on a lack of statistical significance of effects of interest. What is characteristic of our study is that we aimed to obtain the most-precise estimates of within-subject effects, and thus each of our participants completed a procedure including over a thousand trials, allowing us to apply hierarchical statistical models, which are characterized by higher sensitivity than the statistical methods used in previous studies. Most importantly, we performed a Bayesian analysis that allowed us to test for and reliably conclude that the null result was present. Therefore, we think that the discussed methodological improvements we introduced might account for discrepancies between our and previously reported results regarding the influence of attention on VAN.

Our results are, however, in line with the findings of several other studies, which did show that absolute values of ERP waveforms in the VAN time window can be modulated by task requirements (Sun et al., 2023; Andersen et al., 2022; Dellert et al., 2021; Schlossmacher et al., 2020; Schelonka et al., 2017; Shafto & Pitts, 2015; Pitts, Metzler, et al., 2014; Pitts et al., 2012; Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2008; Koivisto, Revonsuo, & Salminen, 2005). Moreover, late VAN was shown to exhibit greater amplitude in response to intrinsically salient stimuli, especially in the hemisphere contralateral to the side on which salient content was presented (Sun et al., 2023; Qiu, Becker, & Pegna, 2022a, 2022b; Zotto & Pegna, 2015), again matching our findings. What constitutes the novelty of our study in terms of the experimental design but was missing in previous inattentional blindness experiments (Sun et al., 2023; Dellert et al., 2021; Schlossmacher et al., 2020; Schelonka et al., 2017;

Shafto & Pitts, 2015; Pitts et al., 2012) is that we included a task-relevant yet unconscious condition. By using such a full factorial design, we were thus able to investigate the interaction between awareness and various dimensions of attentional processing.

We would like to point out two methodological limitations that might have potentially affected the investigated interaction between VAN and attention-related factors. First, considering that the backward masking procedure was used, awareness was not the only difference between the consciously and unconsciously perceived stimuli as they also differed in terms of physical aspects of the stimulation (i.e., presence of a mask). As we neither included mask-only control trials, nor used varying stimulus-mask intervals, we were not able to distinguish the activity evoked by the mask (to subtract it from the neural response to masked faces). As we neither included mask-only control trials, nor used varying stimulus-mask intervals, we were not able to distinguish the activity evoked by the mask (to subtract it from the neural response to masked faces). As the main focus of the present study is on the interaction between awareness and attention-related factors, the confounds introduced by the backward masking procedure are most relevant if the neural activity induced by masks affected the observed interactive effect. The only scenario in which our conclusions regarding this interaction might have been compromised is if in the unconscious condition differences in the ERP responses between attended and unattended stimuli were the same or higher than those observed in the conscious condition, and this could only be possible if ERP values evoked by masks in the task-relevant condition were more positive than in the task-irrelevant condition. We argue that such a pattern of results was highly unlikely as attended stimuli are generally known to evoke more negative ERP values in the VAN time window (Luck, 2012; Luck & Kappenman, 2012). However, this and other potentially confounding effects of the applied masking procedure cannot be excluded based on collected data. Second, differences in low-level visual properties between the images presenting neutral and emotional facial expressions might constitute potential confounds when analyzing the effects related to exogenous attention (see: Hedger, Adams, & Garner, 2015; Gray, Adams, Hedger, Newton, & Garner, 2013). Although the impact of physical differences cannot be completely refuted, it is worth noticing that a recent study conducted by Bruchmann, Mertens, Schindler, and Straube (2023) revealed that the modulations of ERP amplitudes in both early and late time windows of VAN are most likely related to the holistic perception of facial expression, and cannot be explained by responses to low-level physical features. Most importantly, the confounding effect of physical properties is irrelevant to our conclusions regarding the modulation of VAN introduced by the manipulation of facial expressions, as low-level visual features were shared across stimuli presented in both masking conditions.

Dissociating VAN from the Attention-related Effects

Previous studies have suggested that VAN can be distinguished from attentional processes on the basis of its distinct temporal profile (Koivisto & Revonsuo, 2010). Specifically, the observations that a mere detection of a stimulus is related to earlier negative deflection than identification of a stimulus (Koivisto, Grassini, Salminen-Vaparanta, & Revonsuo, 2017) and that attention affects VAN only in the late time window (i.e., after 200 msec; Qiu et al., 2022a, 2022b; Zotto & Pegna, 2015; Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2008; Koivisto, Revonsuo, & Salminen, 2005) led to the conclusion that the early part of VAN reflects the elementary phenomenal experience of a stimulus before, and thus independent of, attentional selection, recognition, and semantic analysis (Railo et al., 2011). However, this view is challenged by the modulation of early VAN by task relevance that we observed and, particularly, by its complete suppression in response to nonsalient, task-irrelevant stimuli.

Importantly, one could argue that the finding that the complete absence of VAN in response to nonsalient, task-irrelevant stimuli results from a lack of awareness of these stimuli. Such an argument cannot be easily refuted because subjective measures of phenomenal consciousness (e.g., Perceptual Awareness Scale; Ramsøy & Overgaard, 2004) were not used in the task-irrelevant condition of our study (as the stimuli would then have, by definition, become task-relevant). However, two pieces of evidence indicate that participants consciously perceived the unmasked task-irrelevant face images in our study. First, the behavioral results demonstrate that participants were very accurate in recognizing unmasked faces in the identification task, which makes it unlikely that the same stimuli were completely invisible in the DP task. Second, the DP task was relatively simple, as indicated by the ceiling-level performance and, most importantly, participants were informed that face images would appear in each trial (Doradzińska & Bola, 2023). Thus, neither of the two main conditions that are known to evoke inattentional blindness-a demanding distracting task or an effect of surprise (Hutchinson, Pammer, Bandara, & Jack, 2022; Pitts et al., 2012; Simons & Chabris, 1999)was met in our study. Therefore, in our view, it is highly probable that task-irrelevant (i.e., unattended) stimuli were consciously perceived in our study. Nevertheless, the lack of direct measure of the subjective experience of stimuli presented in the task-irrelevant condition constitutes a crucial limitation of our study, which should be addressed by future work, for instance by using awareness measures in the form of questionnaires at the end of the study.

Although our data clearly show that ERP effects related to attention and awareness cannot be easily dissociated on the basis of their temporal profiles, dissociation based on their spatial features might also not be possible. Inspection of the topographic maps of the investigated ERP

components (Figure 6) shows that VAN exhibits a very similar posterior topography to effects related to attention manipulation. In line with this observation, previous studies indicated the ventral stream of the visual system as the region most likely to generate VAN (Andersen et al., 2022; Kronemer et al., 2022; Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008; Fahrenfort, Scholte, & Lamme, 2007; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006; Pins & Ffytche, 2003) and, importantly, the very same areas have been established as playing a crucial role in the mechanism of visual attention (Fries, 2015; Buffalo et al., 2010; Di Russo, Martínez, & Hillyard, 2003; Reynolds, Pasternak, & Desimone, 2000; Kastner, Pinsk, Weerd, Desimone, & Ungerleider, 1999; McAdams & Maunsell, 1999; Luck et al., 1997; Chelazzi, Miller, Duncan, & Desimone, 1993; Moran & Desimone, 1985). Although conclusions regarding topographic patterns should be interpreted with caution as we did not conduct a sourcelocalization analysis (because of the lack of precise data regarding the location of electrodes and the lack of structural brain scans of participants), we also conducted an additional analysis of VAN recorded on the occipital cluster of electrodes, results of which can be found in the Appendix C. Importantly, in this analysis, VAN was not observed in the early time window, whereas the negative effects observed in the late time window were modulated by endogenous attention. Therefore, our study provides preliminary evidence that early effects of awareness and attention also overlap in the spatial domain.

VAN-like Activity Evoked by Unconscious Stimuli

Finally, our study provides evidence that negative ERP deflection similar to VAN can be observed even in the absence of stimulus awareness. First, when compared with neutral ones, fearful faces evoked more negative ERP values in the task-relevant condition in the early VAN time window; second, task-relevant stimuli, when contrasted with task-irrelevant ones, produced an analogous effect in the late VAN time window. Thus, although suppression of early VAN induced by the manipulation of endogenous attention indicates that this subcomponent is not necessary for awareness, the unconscious VAN-like activity suggests it is also not sufficient for conscious experience to occur.

"Unconscious effects" on ERP amplitudes within the VAN time window have been observed in previous works. Higher amplitude of the N1 component in response to invisible emotional faces, in comparison to neutral ones, has been reported by multiple previous studies (Mudrik & Deouell, 2022; Axelrod et al., 2015; Zotto & Pegna, 2015; Pegna, Darque, Berrut, & Khateb, 2011; Pegna, Landis, & Khateb, 2008; but see Qiu et al., 2022a). Regarding the late VAN time window, Koivisto and Grassini (2016) found a similar deflection evoked by unconsciously perceived stimuli followed by a correct response in the identification task, when compared with



Figure 6. Topographic maps of ERPs in the 70- to 670-msec time window. (A) Potentials averaged across all conditions. (B) Differential potentials resulting from the subtraction of average ERP values in masked and unmasked trials (top row), task-relevant and task-irrelevant trials (middle row), and unmasked fearful and unmasked neutral trials (bottom row). Note that the scale in the bottom row is different from the scales used in other rows.

stimuli that induced an incorrect response. Furthermore, both exogenous attention (e.g., salient self-related stimuli; Bola et al., 2021; Wójcik et al., 2019) and endogenous attention (i.e., task relevance; Travis et al., 2019) to unconscious stimuli resulted in a more pronounced N2 component appearing contralaterally to the attentionally prioritized stimulus (N2pc). Early studies on the influence of attention on VAN also showed that the amplitude of this component was affected by task relevance, regardless of whether the stimulus was visible or not (Koivisto & Revonsuo, 2007; Koivisto et al., 2005), but the authors were reluctant to interpret this result as unconscious VAN-like activity. Altogether, our finding is not unique and it extends the existing body of evidence.

When investigating unconscious effects, the main challenge is to prove the absence of awareness (Mudrik & Deouell, 2022; Axelrod et al., 2015). Considering that the d' index in the masked identification task was significantly

higher than 0, the "unconscious VAN" we observed might have potentially been caused by residual awareness of masked stimuli. Specifically, it might be stated that salient emotional expressions were generally more likely to be perceived consciously, thus explaining the VAN-like effect found in the masked condition of our procedure. However, there are several points indicating that this was not the case. First, we found that the emotion of the face presented on the opposite side of the screen impacted participants' ability to categorize fearful faces in the unmasked condition, but we did not find a similar effect in the masked condition. This observation shows that participants' decisions in the masked condition were not impacted by stimuli appearing on the screen, thus suggesting no conscious recognition. Second, we conducted an additional analysis of the ERP effects observed in the identification task (Appendix D), and the comparison between trials in which a correct response was provided and those in which participants made an incorrect response revealed no differences in the amplitudes of ERP waveforms. Finally, in the late VAN time window, we found no signs of attentional prioritization of masked fearful faces, although they have very strong attention-grabbing properties when perceived consciously (Doradzińska & Bola, 2023). Altogether, this evidence suggests that the VAN-like activity could be an effect of unconscious assessment and, potentially, attentional prioritization of perceptual information.

Theoretical Implications, Potential Mechanisms, and Future Directions

VAN is mainly interpreted in the context of (and is considered to provide support for) RPT (Lamme, 2006, 2010). According to RPT, activity of local feedback projections in the modality-specific sensory cortex generates awareness (Lamme, 2003, 2004), and PAN reflects this mechanism at the scalp level (Lamme, 2018; Snyder, Yerkes, & Pitts, 2015; Meyer, 2011). Importantly, RPT assumes that phenomenal experience is independent of the processes related to attentional selection (Lamme, 2004). Thus, by showing attentional modulation of VAN, our study challenges RPT and suggests that this theory should either abandon the assumption that consciousness and attention are independent (in line with Graziano, 2022; Cohen, Cavanagh, Chun, & Nakayama, 2012; O'Regan & Noë, 2001), or it should develop a more precise definition of the neural mechanism of awareness that would allow it to be distinguished from neural activity related to attentional selection.

Finally, our results bring new insights to the ongoing discussion about the timing and location of NCC (Boly et al., 2017). VAN is considered an NCC by proponents of the "early and posterior" mechanism of consciousness, whereas supporters of the "late and frontal" mechanism claim that neural processes that give rise to perceptual awareness are related to global brain activations, including parietal and frontal cortical regions, thus proposing that the P3b ERP component is a putative index of consciousness (Dehaene & Changeux, 2011). Although both sides of this dispute seem to have provided extensive evidence supporting their claims, a recent meta-analysis revealed that, in general, this research field continues to provide evidence that corroborates already established models but lacks both critical examination and falsification of theoretical predictions (Yaron, Melloni, Pitts, & Mudrik, 2022). Indeed, one of the most important contributions to this field came from studies aiming to falsify the role of P3b as a potential NCC by showing it is neither necessary (Dellert, Krebs et al., 2022; Kronemer et al., 2022; Dellert, Müller-Bardorff et al., 2021; Schlossmacher et al., 2021; Schröder et al., 2021; Sergent et al., 2021; Cohen et al., 2020; Koivisto et al., 2016; Pitts, Metzler et al., 2014; Pitts, Padwal et al., 2014; also supported also by our results) nor sufficient for a conscious experience to occur (however,

the latter observation requires further evidence; Doradzińska et al., 2020; Silverstein, Snodgrass, Shevrin, & Kushwaha, 2015). We recently postulated that a similar approach should be applied to VAN and, more generally, PAN (Bola & Doradzińska, 2021). In the present study, we provide results suggesting that VAN indeed cannot be treated as a pure and specific NCC. Thus, although our data do not refute the "early and posterior" hypothesis, our findings do indicate that VAN, at least to some extent, reflects perceptual and cognitive processes. Furthermore, it is our opinion that disentangling neural activity responsible for awareness and attention using standard neuroimaging methods such as ERPs might be impossible.

Conclusions

To conclude, our study provides robust evidence that VAN is modulated and, at its early stages, even gated by attentional mechanisms, and VAN-like ERP waveforms can be induced by attentional prioritization, even in the condition of perceptual unawareness. By showing that VAN is not specific and, in the early time window, also not necessary for awareness, our findings indicate that rather than being a marker of phenomenal experience, the mechanism that generates VAN is closely related to attentional prioritization.

APPENDIX A: THE ANALYSIS OF THE MODULATION OF d' AND CRITERION BY THE EXPRESSION OF ACCOMPANYING FACE

Data Analysis

In the present analysis, we extended the approach from the original study (Doradzińska & Bola, 2023) by examining the influence of expressions of faces presented on one side of the screen (i.e., not followed by the asterisks) on the ability to recognize emotions expressed on faces presented on the other side i.e., followed by the asterisks). Behavioral data processing was conducted using custom-made Python scripts. Similarly, as in the original study, we excluded no-response trials from the analysis, which resulted in a median of 571 out of 576 ID trials left per participant (range = [454,576]). First, we divided trials depending on the masking condition (i.e., masked or unmasked). Further trials were grouped based on the emotion (fearful or neutral) expressed by the face presented together with the face that participants had to categorize (i.e., on the opposite side of the screen). For each participant, we have calculated d' and c values separately for each combination of masking and the accompanying facial expression. Extreme values of the d' parameter were corrected using the "1/(2 N) rule" (Hautus, 1995). Obtained STD parameters entered the statistical analysis.

Statistical Analysis

The statistical tests that were used to evaluate the behavioral results were performed using the open-source JASP 0.15 software (JASP Team, 2021). The signal-detection theory parameters obtained in the ID task were described with means (M) and standard deviations (SD) and were introduced to repeated-measures Type III ANOVA with two two-level factors: second face (emotion on the face presented on the opposite side of the screen that the following pair of asterisks; neutral or fearful) and masking (masked or unmasked condition). The statistic was reported as F(df), together with the indicator of the effect size, partial eta-squared, reported as η_p^2 . Interactions were resolved with contrasts and reported as t(df). For all tests, probability values were reported as p, and the threshold alpha level for refuting the null hypothesis was set to the standard of .05.

Results

We investigated to what extent the ability to recognize the emotion of the face followed by the asterisks is impacted by two factors: masking and second face, defined as the expression of the face presented on the opposite side of the screen. The ANOVA conducted on d' index values revealed a significant main effect of masking, F(1, 40) = $378.55, p < .001, \eta_p^2 = .821$; significant main effect of second face, $F(1, 40) = 15.66, p < .001, \eta_p^2 = .015$; and significant interaction between those two factors, F(1, 40) = $6.81, p = .013, \eta_p^2 = .006$. Unsurprisingly, the masked condition was related to overall lower d' values than the unmasked condition (masked, estimation of marginal means [EMM] = 0.10, CI [-0.1, 0.22]; unmasked, EMM = 1.56, CI [1.45, 1.68]). Fearful expression of the accompanying face resulted in a lower d' index, but contrast analysis indicated that this effect was significant only in the unmasked condition, masked, t(40) = 1.70, p = .098; unmasked, t(40) = 3.77, p < .001; unmasked neutral, EMM = 1.72, CI [1.59, 1.86]; unmasked fearful, EMM =1.40, CI [1.27, 1.54]. Obtained results indicate that in the unmasked condition, the fearful expression of accompanying face suppressed the ability of participants to identify the emotion expressed by the target face.

We investigated the same factors in ANOVA performed on criterion values, and we found the significant main effect of masking, F(1, 40) = 18.18, p < .001, $\eta_p^2 = .195$, and significant interaction between masking and the second face, F(1, 40) = 8.58, p = .006, $\eta_p^2 = .024$. In the masked condition, criterion values were overall higher than in the unmasked condition (masked, EMM = 0.32, CI [0.19, 0.45]; unmasked, EMM = -0.05, CI [-0.13, 0.04]), which means that when faces were followed by masks, participants were more likely to respond that the facial expression was neutral. Furthermore, the analysis of contrasts showed that in the unmasked condition, criterion values were higher when the expression of the accompanying face was fearful (EMM = 0.06 CI [-0.11, 0.26]) than when it was neutral (EMM = -0.16, CI [-0.23, -0.08]; t(40) = -2.13, p = .039). This effect was not observed in the masked condition, t(40) = 1.15, p = .256. These results suggest that when the visibility of faces was suppressed (i.e., in the masked condition), participants were more likely to indicate that a presented face was neutral. When faces were not masked (i.e., easily visible), participants' bias was affected by the expression of the accompanying face. Specifically, participants were more prone to respond that the face was fearful when it was accompanied by a neutral face than when it was accompanied by a fearful face.

APPENDIX B: THE FREQUENTIST ANALYSIS OF VAN ON POSTERIOR TEMPORAL ELECTRODES

Data Analysis

Analyses were conducted on the same data sets as Bayesian analysis presented in the main body of this article. Before fitting the model, trials in which components' amplitudes exceeded 3 *SD*s from the mean were excluded from each data set (less than 0.9% of values).

Statistical Analysis

ERP effects were statistically evaluated using mixed linear models. The analysis was conducted in RStudio 1.4.1717 (RStudio Team, 2021) using R programming language (R Core Team, 2021). Mixed linear models were fitted to ERP data using the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015) and were evaluated with the "lmerTest" package (Kuznetsova, Brockhoff, & Christensen, 2017) and the "emmeans" package (Lenth, 2024).

In each time window of VAN, ERP values were analyzed using two types of models. The first one included the general effect of emotional expression, and the fixed-effects structure contained three 2-level factors: masking (masked or unmasked condition), emotion (fearful or neutral), and task relevance (task-relevant or taskirrelevant condition; trials from the ID or DP tasks, respectively). The second one accounted for the lateralized effect of spatial attention reaction to the emotional face presented on one side of the screen and had the same 2 \times 2×2 fixed-effects design, but instead of emotion, we included a factor of side (amplitude obtained ipsilaterally or contralaterally, with respect to the side of the fearful face presentation). The random-effect structure was specified separately for each time window of VAN and each model, starting with the maximal model (Barr, Levy, Scheepers, & Tily, 2013) and performing the iterative reduction of model complexity until all linear combinations of remaining random effects were estimated to have nonzero variability (i.e., the fitted models are not singular; Bates, Kliegl, Vasishth, & Baayen, 2018). All models

selected in this fashion were significantly better than the model containing only the random intercept (comparison was evaluated based on the Akaike information criterion—of the selected model and a random intercept model). Fixed effects were evaluated with a Type III ANOVA, and the obtained results were reported as F(df). In the case of significant effect, the follow-up analysis consisted of an EMM to obtain the direction of effects. The interactions were resolved with contrasts, which were calculated using Satterthwaite's method for estimating denominator degrees of freedom (Luke, 2017; Satterthwaite, 1941), and they were reported as t(df). p Values calculated for more than two contrasts were corrected for multiple comparisons with the Holm–Bonferroni method (Holm, 1979).

ERP Results

Early VAN (N1 Time Window)

The first analysis of VAN in the early time window included the emotion factor (on trials with two fearful or two neutral faces). It was conducted with a model containing random intercept and random slopes of masking and task relevance. The ANOVA performed on fixed effects showed a significant main effect of masking, F(1, 40.0) = 7.57, p =.009, and a significant interaction of masking and task relevance, F(1, 21136.8) = 4.40, p = .036. Follow-up contrasts indicated that the effect of masking was significant only in the task-relevant condition, t(55.7) = 3.34, p =.002, with unmasked trials resulting with lower ERP values than masked trials (masked, EMM = $-2.85 \,\mu$ V, CI [$-3.75 \,\mu$ V, $-1.89 \,\mu\text{V}$; unmasked, EMM = $-3.52 \,\mu\text{V}$, CI [$-4.38 \,\mu\text{V}$, $-2.66 \,\mu\text{V}$), whereas in the task-irrelevant condition, the difference between masked and unmasked trials did not reached statistical significance, t(54.4) = 1.74, p = .088; masked, EMM = $-2.54 \,\mu\text{V}$, CI [$-3.28 \,\mu\text{V}$, $-1.80 \,\mu\text{V}$]; unmasked, EMM = $-2.91 \,\mu\text{V}$, CI [$-3.60 \,\mu\text{V}$, $-2.21 \,\mu\text{V}$]. In addition, we found a significant main effect of emotion, F(1, 21127.7) = 13.05, p < .001, with fearful trials evoking generally more negative values of ERP than neutral ones (fearful, EMM = $-3.09 \,\mu\text{V}$, CI [$-3.85 \,\mu\text{V}$, $-2.33 \,\mu\text{V}$]; neutral, EMM = $-2.80 \,\mu\text{V}$, CI [$-3.56 \,\mu\text{V}$, $-2.04 \,\mu\text{V}$]) and a significant main effect of task relevance, F(1, 40.1) =4.84, p = .034. The analysis of contrasts revealed that task-relevant faces evoked significantly more negative potentials when compared with task-irrelevant ones in the unmasked condition only, masked, t(54.0) = 1.27, p = .209; unmasked, t(53.4) = 2.82, p = .007. Overall, the pattern of results indicated that early VAN was present in the task-relevant condition and not found in the task-irrelevant one. Furthermore, contrasting fearful and neutral trials resulted in a VAN-like effect that was present regardless of stimulus visibility.

The second analysis, investigating lateralized ERP responses in trials containing one fearful and one neutral face, was done using a model with a random intercept and

random effects of masking, task relevance, and the interaction between those two factors. The ANOVA on fixed effects revealed a significant main effect of masking, F(1,40) = 9.84, p = .003, and a significant interaction between masking and task relevance, F(1, 40) = 5.52, p = .024. The analysis of contrasts showed that the unmasked stimuli evoked lower values of ERPs, but this effect was significant in the task-relevant condition, t(40.2) = 3.79, p < .001; masked, EMM = $-2.71 \,\mu\text{V}$, CI [$-3.60 \,\mu\text{V}$, $-1.82 \,\mu\text{V}$]; unmasked, EMM = $-3.39 \,\mu\text{V}$, CI [$-4.22 \,\mu\text{V}$, $-2.56 \,\mu\text{V}$], and not in the task-irrelevant condition, t(40.4) = 1.51, p = .139; masked, EMM = $-2.61 \mu V$, CI [$-3.29 \mu V$, $-1.93 \,\mu\text{V}$; unmasked, EMM = $-2.87 \,\mu\text{V}$, CI [$-3.29 \,\mu\text{V}$, $-2.19 \,\mu\text{V}$]. Apart from that, we also found a significant main effect of side, F(1, 42392) = 12.30, p < .001, with more negative potentials registered contralaterally to fearful face presentation (ipsi, EMM = -2.78μ V, CI $[-3.52 \ \mu\text{V}, -2.05 \ \mu\text{V}]$; contra, EMM = $-3.01 \ \mu\text{V}$, CI $[-3.74 \,\mu\text{V}, -2.27 \,\mu\text{V}]$). In summary, we again found early VAN only in the task-relevant condition and VAN-like lateralized effect contralaterally to the side of fearful face presentation in both masking conditions.

Late VAN (P2-N2 Time Window)

For the analysis of ERP values collected in the late time window in trials containing two fearful or two neutral faces (constituting emotion factor), a model containing random intercept and random slopes of task relevance and masking was selected. ANOVA conducted for fixed effects revealed a significant effect of masking, F(1, 40.4) =191.31, p < .001, as well as significant two-way interactions between masking and task relevance, F(1, 21129.4) =52.64, p < .001, and between masking and emotion, F(1, 21104.8) = 4.67, p = .031. A follow-up contrast analysis indicates that the effect of masking was significant in both task relevance conditions, task-relevant: t(60.6) =15.55, p < .001; task-irrelevant: t(59.1) = 9.50, p < 0.001.001, with unmasked trials resulting in lower ERP values than masked trials. Furthermore, the masking effect was stronger in the task-relevant condition (masked, EMM = $2.51 \,\mu\text{V}, \text{CI} [1.63 \,\mu\text{V}, 3.39 \,\mu\text{V}]; \text{ unmasked}, \text{EMM} = -0.50 \,\mu\text{V},$ CI $[-1.26 \,\mu\text{V}, 0.26 \,\mu\text{V}])$ compared with the task-irrelevant condition (masked, EMM = $3.50 \,\mu\text{V}$, CI [$2.74 \,\mu\text{V}$, $4.26 \,\mu\text{V}$]; unmasked, EMM = $1.67 \,\mu\text{V}$, CI [$1.16 \,\mu\text{V}$, $2.19 \,\mu\text{V}$]). Similarly, the negative difference between ERPs obtained from masked and unmasked trials was present in both emotion conditions, fearful, t(59.8) = 13.45, p < .001; neutral, t(59.9) = 11.62, p < .001, but the difference was greater for fearful faces (masked, EMM = 3.02μ V, CI [2.25 μ V, 3.79 μ V]; unmasked, EMM = 0.43 μ V, CI [-0.15 μ V, 1.01 μ V]) than for neutral ones (masked, EMM = 2.99 μ V, CI $[2.22 \ \mu\text{V}, 3.76 \ \mu\text{V}];$ unmasked, EMM = 0.75 \ \mu\text{V}, CI $[0.17 \ \mu\text{V}, 1.33 \ \mu\text{V}]$). In addition, we found a significant main effect of the task relevance, F(1, 40.2) = 28.73, p < .001. Contrast analysis conducted separately for masked and unmasked faces showed that ERP values obtained in the task-relevant condition were generally lower than those obtained in the task-irrelevant condition, masked, t(46.7) = 3.23, p = .002; unmasked, t(46.5) = 7.10, p < .001. Thus obtained results indicate that late VAN was present in all attentional conditions; however, its amplitude was attenuated when stimuli were nonsalient or task-irrelevant. Moreover, the manipulation of task relevance was associated with the effect resembling VAN for both masked and unmasked faces.

For the analysis that included the effect of lateralization in response to trials with one fearful and one neutral face, a model with a random intercept, random slopes of task relevance and masking, and random slope of the interaction between masking and task relevance was used. ANOVA on fixed effects resulted in a significant main effect of masking, F(1, 40.0) = 174.18, p < .001, and significant two-way interactions between masking and task relevance, F(1,40.0) = 29.14, p < .001, and between masking and side, F(1, 42379) = 29.80, p < .001. Contrast analysis showed that in both tasks, unmasked trials evoked lower potentials than masked trials, task-relevant: t(40.0) = 11.45, p < .001;task-irrelevant: t(40.2) = 10.72, p < .001, and the effect of masking was stronger for task-relevant (masked: EMM = 2.58 μ V, CI [1.74 μ V, 3.42 μ V]; unmasked: EMM = -0.36 μ V, CI $[-1.18 \,\mu\text{V}, 0.46 \,\mu\text{V}]$) compared with task-irrelevant condition (masked: EMM = $3.32 \,\mu\text{V}$, CI [2.58 μV , 4.05 μV]; unmasked: EMM = $1.68 \mu V$, CI [$1.08 \mu V$, $2.28 \mu V$]). Furthermore, unmasked trials resulted in significantly lower potentials than masked trials, regardless of the side, contralateral: t(51.4) = 14.27, p < .001; ipsilateral: t(51.4) =10.52, p < .001, but the stronger effect of masking was registered on contralateral electrodes (masked: EMM = 3.00 μ V, CI [2.25 μ V, 3.75 μ V]; unmasked: EMM = 0.36 μ V, CI $[-0.28 \,\mu\text{V}, 1.00 \,\mu\text{V}])$ in comparison to ipsilateral sites (masked: EMM = $2.90 \,\mu\text{V}$, CI [$2.15 \,\mu\text{V}$, $3.65 \,\mu\text{V}$]; unmasked: EMM = 0.95 μ V, CI [0.31 μ V, 1.59 μ V]). Therefore this analysis resulted in the pattern of results suggesting that VAN was present in all attention-related conditions, but both task relevance and stimulus saliency had an impact on its amplitude.

APPENDIX C: THE BAYESIAN ANALYSIS OF ERP AMPLITUDES IN OCCIPITAL CLUSTER OF ELECTRODES

Data Analysis

Only trials containing two fearful or two neutral faces entered the analysis. For each of the early and late VAN time windows, we calculated the mean amplitude of EEG signal pooled from the following electrodes PO3, POz, PO4, O1, Oz, and O2. This was done for each epoch separately, and values obtained for all participants were pooled together in two arrays (one for each time window), each consisting of 21,359 data points, which entered statistical analysis.

Statistical Analysis

ERP effects were statistically evaluated using Bayesian mixed models and the same procedure of model assessment as described in the main body of the article. Models used for the analysis of VAN recorded in the occipital cluster contained three population-level factors: masking (masked or unmasked), task relevance (task-relevant and task-irrelevant) and emotion (fearful or neutral). All models contained a maximal random effect structure including a random intercept of participants and random slopes of all considered population-level effects and their interactions, and the maximal structure of fixed effects. We report the evidence ratio for the one-sided hypotheses about the differences between conditions (Evid. $Ratio_1$), and in case of small values (i.e., not exceeding 95% CI) also the evidence ratio for two-sided hypotheses of two conditions being equal (Evid. Ratio₀).

ERP Results

Early VAN in the Occipital Cluster

In the occipital cluster of electrodes the early VAN was not present and in fact, instead of a negative, we observed a positive differential potential when comparing the response to unmasked stimuli to the response to masked ones. This was true for both types of stimuli and both task relevance conditions (task-irrelevant neutral: masked, $M = -1.42 \,\mu\text{V}$, CI [-2.29 μ V, -0.50 μ V], unmasked, M = $0.79 \,\mu\text{V}$, CI [$-0.73 \,\mu\text{V}$, 1.63 μV], Evid. Ratio₁ > 8000; taskirrelevant fearful: masked, $M = -1.02 \mu V$, CI [-1.92 μV , $-0.10 \ \mu V$], unmasked, $M = 0.70 \ \mu V$, CI [$-0.17 \ \mu V$, 1.56 μ V], Evid. Ratio₁ > 8000; task-relevant neutral: masked, $M = -1.22 \ \mu V$, CI [-2.25 μV , -0.19 μV], unmasked, $M = -0.31 \,\mu\text{V}$, CI $[-0.63 \,\mu\text{V}, 1.23 \,\mu\text{V}]$, Evid. Ratio₁ = 3999.00; task-relevant fearful: masked, M = $-1.30 \,\mu\text{V}$, CI [$-2.36 \,\mu\text{V}$, $-0.23 \,\mu\text{V}$], unmasked, M =0.28 μ V, CI [-0.79 μ V, 1.31 μ V], Evid. Ratio₁ > 8000). The amplitude of this positive differential potential was not influenced by the emotion expressed on faces (taskirrelevant, Evid. Ratio₁ = 17.78, Evid. Ratio₀ = 66.62; task-relevant, Evid. Ratio₁ = 0.79, Evid. Ratio₀ = 341.93), but we found an interaction between the effect of masking and task relevance. Specifically, neutral task-relevant faces produced lower awareness-related positivity than neutral task-irrelevant ones (Evid. Ratio₁ = 65.12). This effect was not present for fearful faces (Evid. $Ratio_1 = 2.04$, Evid. $Ratio_0 = 307.57$).

When exploring the effects of facial expression and task on absolute ERP values, we discovered that neither the factor of emotion (task-irrelevant masked, Evid. Ratio₁ = 0.03, Evid. Ratio₀ = 63.88; task-relevant masked, Evid. Ratio₁ = 1.75, Evid. Ratio₀ = 435.69; task-irrelevant unmasked, Evid. Ratio₁ = 1.99, Evid. Ratio₀ = 459.89; task-relevant unmasked, Evid. Ratio₁ = 1.21, Evid. Ratio₀ = 617.59) nor task relevance (neutral masked, Evid. Ratio₁ = 0.34, Evid. Ratio₀ = 195.05; fearful masked, Evid. Ratio₁ = 5.14, Evid. Ratio₀ = 229.25; neutral unmasked, Evid. Ratio₁ = 16.09, Evid. Ratio₀ = 110.82; fearful unmasked, Evid. Ratio₁ = 9.30, Evid. Ratio₀ = 207.09) were related with reliable differences in recorded potentials.

Overall, we did not observe awareness related negativity in the occipital cluster in the early time window. Furthermore, the pattern of results suggests that salient and taskirrelevant stimuli produced positive awareness-related effects higher than other types of stimuli; however, those differences are very low, as they were captured only in the comparison between nonsalient task-irrelevant and nonsalient task-relevant conditions. We found no other modulations of ERP amplitudes in this time window.

Late VAN in the Occipital Cluster

In the late time window, VAN was present in the occipital cluster in all experimental conditions (task-irrelevant neutral: masked, $M = 5.09 \,\mu\text{V}$, CI [4.12 μV , 6.02 μV], unmasked, $M = 2.79 \,\mu\text{V}, \text{CI} [1.96 \,\mu\text{V}, 3.59 \,\mu\text{V}], \text{Evid. Ratio}_1 > 8000; \text{ task-}$ irrelevant fearful: masked, $M = 5.32 \,\mu\text{V}$, CI [4.36 μV , 6.29 μV], unmasked, $M = 2.86 \,\mu\text{V}$, CI [2.04 μ V, 3.66 μ V], Evid. Ratio₁ > 8000; task-relevant neutral: masked, $M = 5.22 \,\mu\text{V}$, CI [4.05 μ V, $6.37 \,\mu\text{V}$, unmasked, $M = 1.89 \,\mu\text{V}$, CI [0.87 μV , 2.95 μV], Evid. Ratio₁ > 8000; task-relevant fearful: masked, $M = 5.10 \,\mu\text{V}$, CI [3.94 μ V, 6.27 μ V], unmasked, $M = 2.19 \mu$ V, CI [1.07 μ V, 3.33 μ V], Evid. Ratio₁ > 8000). Furthermore, we did not observe the influence of emotional expression on the amplitude of awareness-related negativity, neither in task-irrelevant (Evid. $Ratio_1 = 2.58$, Evid. $Ratio_0 =$ 222.75) nor in the task-relevant condition (Evid. Ratio₁ = 0.11, Evid. Ratio₀ = 138.16). Task relevance impacted the amplitude of VAN, but only in trials in which neutral faces were presented (neutral, Evid. Ratio₁ = 7999.00; fearful, Evid. Ratio₁ = 10.68, Evid. Ratio₀ = 126.89).

The absolute values of ERP waveform evoked by fearful and neutral faces did not differ, and this was true in all combinations of masking and task relevance (task-irrelevant masked, Evid. Ratio₁ = 0.14, Evid. Ratio₀ = 188.90; taskrelevant masked, Evid. Ratio₁ = 2.43, Evid. Ratio₀ = 418.50; task-irrelevant unmasked, Evid. Ratio₁ = 0.56, Evid. $Ratio_0 = 486.40$; task-relevant unmasked, Evid. $Ratio_1 = 0.14$, Evid. $Ratio_0 = 297.29$). As for the influence of task relevance, we observed that only in the unmasked condition and only for neutral faces task-relevant condition was related to lower ERP values than the taskirrelevant condition (Evid. $Ratio_1 = 69.18$), and this effect was absent for all other combinations of emotion and masking (neutral masked, Evid. Ratio₁ = 0.54, Evid. $Ratio_0 = 177.21$; fearful masked, Evid. $Ratio_1 = 2.42$, Evid. $Ratio_0 = 220.08$; fearful unmasked, Evid. $Ratio_1 = 14.21$, Evid. Ratio₀ = 106.98).

Our results indicate that conscious perception of all types of stimuli was related with a pronounced late VAN in the occipital cluster. At the same time, we found some evidence that the highest amplitude of VAN might be obtained for nonsalient, but task-relevant stimuli. This effect was captured in the comparison of VAN amplitudes between task-irrelevant and task-relevant conditions, and in the comparison of absolute ERP values between unmasked task-relevant and task-irrelevant conditions. Our model did not capture the effect of task relevance on VAN evoked by fearful faces; however, it can be explained by the proximity of occipital cluster to parietal regions on which the P3b component was recorded. Noteworthy, the analysis of P3b revealed the enhanced positivity at response to unmasked fearful faces, when compared with neutral stimuli, and perhaps this effect was already present in the late VAN time window and impacted ERP values recorded in the occipital region.

APPENDIX D: THE BAYESIAN ANALYSIS OF ERP AMPLITUDES IN POSTERIOR TEMPORAL CLUSTER CONDUCTED IN MASKED CONDITION WITH REGARD TO RESPONSES IN ID TASK

Data Analysis

From the data sets used for Bayesian analysis of VAN in posterior temporal cluster (already filtered for outliers), we picked datapoints collected from masked trials in the identification task. Therefore the amount of data points entering the analysis of the early VAN time window was 5151 for nonlateralized effects and 10,310 for the lateralized effects. The analysis of ERP values in the late VAN time window was conducted on 5148 datapoints in case of nonlateralized effects and 10,314 in case of lateralized effects.

Statistical Analysis

ERP effects were statistically evaluated using Bayesian mixed models and the same procedure of model assessment as described in the main body of the article.

To analyze the impact of responses on ERP amplitudes, we fitted data with linear Gaussian models with identity link function. Models used for the analyses nonlateralized ERP effects contained two population-level factors: emotion (fearful or neutral) and response (correct or incorrect), whereas the analysis of lateralized effects included factors of side (ipsilaterally or contralaterally with respect to the side of the fearful face presentation) and response (correct and incorrect). All models contained a maximal random effect structure including a random intercept of participants and random slopes of all considered population-level effects and their interactions. In each analysis, we checked for the presence or absence of the effect induced by the response on all levels of emotion or side, and the differences between fearful and neutral faces or ipsilateral and contralateral hemispheres in trials in which correct responses were made. We report the estimates (M) with 95% confidence intervals (CI) derived

from the model and the evidence ratio speaking against differences between conditions (Evid. Ratio₀).

ERP Results

Early VAN Time Window

For the analysis of ERP values collected in the early VAN time window in trials containing two fearful or two neutral faces, we chose the maximal model, thus the one containing fixed effects of emotion and response as well as the interaction between them. The investigation of the influence of response type on the amplitude of ERP signal revealed that ERP values were not impacted by responses neither in trials in which two fearful faces (correct, M = $-2.79 \ \mu\text{V}$, CI [$-3.79 \ \mu\text{V}$, $-1.80 \ \mu\text{V}$]; incorrect, M = $-2.51 \ \mu\text{V}$, CI [$-3.54 \ \mu\text{V}$, $-1.45 \ \mu\text{V}$]; Evid. Ratio₀ = 126.23), nor when two neutral faces were presented $(\text{correct}, M = -2.09 \,\mu\text{V}, \text{CI} [-4.06 \,\mu\text{V}, -2.09 \,\mu\text{V}]; \text{ incor-}$ rect, $M = -2.88 \,\mu\text{V}$, CI [-3.92 μV , -1.86 μV]; Evid. $Ratio_0 = 234.41$). Furthermore ERP values in trials in which participants gave a correct responses did not differ between fearful and neutral faces (Ratio₀ = 108.60).

When analyzing lateralized ERP responses coming from trials with one fearful and one neutral face, it occurred that the model best fitted our data was the one containing only the intercept and the random effects. In other words, models that included fixed effects of side and response performed substantially worse that the intercept model (ELPD distance from the best model exceeded 2 SEs). Nevertheless, we checked the impact of the response factor in the maximal model (containing fixed effects of side and response, and their interaction), and found that according to this model, the type of response did not affect the ERP values neither in ipsilateral (correct, $M = -2.69 \mu V$, CI [$-3.59 \,\mu\text{V}$, $-1.74 \,\mu\text{V}$]; incorrect, $M = -2.60 \,\mu\text{V}$, CI $[-3.54 \,\mu\text{V}, -1.60 \,\mu\text{V}]$; Evid. Ratio₀ = 278.30) nor in the contralateral hemisphere (correct, $M = -2.66 \mu$ V, CI $[-3.58 \ \mu\text{V}, -1.71 \ \mu\text{V}]$; incorrect, $M = -2.81 \ \mu\text{V}$, CI $[-3.79 \,\mu\text{V}, -1.80 \,\mu\text{V}]$; Evid. Ratio₀ = 345.34). The analysis of trials in which participants provided a correct response revealed that there were no differences between ipsilateral and contralateral hemispheres (Evid. $Ratio_0 =$ 388.87).

Overall, we concluded that responses made in the identification task did not influence the ERP values collected in the early time window of VAN in masked condition. Furthermore, similarly as in the main analysis, there was no effect related to the emotions expressed by presented faces in trials in which a correct response was made.

Late VAN Time Window

In the late VAN time window, the all models containing fixed effects of emotion or response performed worse than the intercept model (ELPD distance from the best model exceeded 2 *SEs*). However, we looked into the

estimated provided by the maximal model, which included population-level effects of emotion and response as well as their interaction. We found that responses did not impact the amplitude of ERP waveform neither for neutral (correct, $M = 2.59 \,\mu$ V, CI [1.65 μ V, 3.49 μ V]; incorrect, $M = 2.58 \,\mu$ V, CI [1.60 μ V, 3.54 μ V]; Evid. Ratio₀ = 232.16) nor for fearful faces (correct, $M = 2.41 \,\mu$ V, CI [1.45 μ V, 3.33 μ V]; incorrect, $M = 2.58 \,\mu$ V, CI [1.56 μ V, 3.56 μ V]; Evid. Ratio₀ = 266.58). In trials in which correct responses were collected, there were no difference between fearful and neutral faces in the amplitudes of ERP waveforms (Evid. Ratio₀ = 201.43).

For the analysis of lateralized effects in the late VAN time window, we picked the only model containing a response factor that did not perform worse than the best one, which was the intercept model. This model was the one containing fixed effects of response and side, but not the interaction between those factors. The investigation of the impact of responses on the ERP amplitude revealed that absolute ERP values were the same regardless whether a correct or incorrect response was made (correct, M =2.51 μ V, CI [1.63 μ V, 3.39 μ V]; incorrect, $M = 2.54 \mu$ V, CI $[1.64 \,\mu\text{V}, 3.45 \,\mu\text{V}]$; Evid. Ratio₀ = 388.07). According to the model, the interaction between response and side was not present in the data; thus, we investigated only the general differences between the ipsilateral and contralateral hemispheres and obtained evidence indicating null effect (ipsi, $M = 2.51 \,\mu\text{V}, \text{CI} [1.63 \,\mu\text{V}, 3.39 \,\mu\text{V}]; \text{ contra}, M = 2.62 \,\mu\text{V},$ CI [1.76 μ V, 3.49 μ V]; Evid. Ratio₀ = 341.51).

Summarizing, also in the late VAN, time window responses made in the identification task did not influence the ERP potentials registered in the masked condition on the posterior temporal cluster of electrodes. Furthermore, the analysis of trials in which correct responses were made shows that the ERP values in masked trials were not influenced by the emotions of presented faces, which is in agreement with the results provided in the main section of the article.

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Data Availability Statement

The scripts used to run the experimental procedure, behavioral and EEG data, and statistical models can be downloaded from OSF repositories (scripts, raw recordings, cleaned and epoched data, and mne.Evoked instances from https://osf.io/46cuq/; behavioral and ERP data in long format, which entered statistical analysis, and statistical models from https://osf.io/t63hw/). The Python and R scripts used for data preprocessing and statistical analysis and a custom Python package containing all used functions can be downloaded from Github (scripts, https://github.com/Lucja-Doradzinska/VAN_ff_prep

_scripts; package, https://github.com/Lucja-Doradzinska /erp_exp_ld).

Author Contributions

Łucja Doradzińska: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Validation; Visualization; Writing—Original draft preparation. Michał Bola: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Note

1. ID's of selected pictures: 02F_NE_C, 02F_FE_O, 03F_NE_C, 03F_FE_O, 05F_NE_C, 05F_FE_O, 06F_NE_C, 06F_FE_O, 07F_NE_C, 07F_FE_O, 08F_NE_C, 08F_FE_O, 09F_NE_C, 09F_FE_O, 10F_NE_C, 10M_FE_O, 20M_NE_C, 20M_FE_O, 21M_NE_C, 21M_FE_O, 24M_NE_C, 24M_FE_O, 25M_NE_C, 25M_FE_O, 27M_NE_C, 27M_FE_O, 28M_NE_C, 28M_FE_O, 33M_NE_C, 33M_FE_O, 34M_NE_C, 34M_FE_O.

REFERENCES

- Andersen, L. M., Pedersen, M. N., Sandberg, K., & Overgaard, M. (2016). Occipital MEG activity in the early time range (< 300 ms) predicts graded changes in perceptual consciousness. *Cerebral Cortex*, *26*, 2677–2688. https://doi.org/10.1093 /cercor/bhv108, PubMed: 26009612
- Andersen, L. M., Vinding, M. C., Sandberg, K., & Overgaard, M. (2022). Task requirements affect the neural correlates of consciousness. *European Journal of Neuroscience*, 56, 5810–5822. https://doi.org/10.1111/ejn.15820, PubMed: 36086829

- Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*, 737–746. https://doi.org/10.1016/j .neubiorev.2011.12.003, PubMed: 22192881
- Auksztulewicz, R., & Blankenburg, F. (2013). Subjective rating of weak tactile stimuli is parametrically encoded in event-related potentials. *Journal of Neuroscience*, 33, 11878–11887. https://doi.org/10.1523/JNEUROSCI.4243-12 .2013, PubMed: 23864677
- Auksztulewicz, R., Spitzer, B., & Blankenburg, F. (2012). Recurrent neural processing and somatosensory awareness. *Journal of Neuroscience*, *32*, 799–805. https://doi.org/10 .1523/JNEUROSCI.3974-11.2012, PubMed: 22262878
- Axelrod, V., Bar, M., & Rees, G. (2015). Exploring the unconscious using faces. *Trends in Cognitive Sciences*, 19, 35–45. https://doi.org/10.1016/j.tics.2014.11.003, PubMed: 25481216
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68, 255–278. https://doi.org/10.1016/j.jml.2012.11.001, PubMed: 24403724
- Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2018). Parsimonious mixed models. *arXiv*. https://doi.org/10.48550 /arXiv.1506.04967
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. https://doi.org/10.18637/jss.v067.i01
- Bola, M., & Doradzińska, Ł. (2021). Perceptual awareness negativity—Does it reflect awareness or attention? *Frontiers in Human Neuroscience*, *15*, 742513. https://doi.org/10.3389 /fnhum.2021.742513, PubMed: 34720911
- Bola, M., Paź, M., Doradzińska, Ł., & Nowicka, A. (2021). The self-face captures attention without consciousness: Evidence from the N2pc ERP component analysis. *Psychophysiology*, *58*, e13759. https://doi.org/10.1111/psyp.13759, PubMed: 33355938
- Boly, M., Massimini, M., Tsuchiya, N., Postle, B. R., Koch, C., & Tononi, G. (2017). Are the neural correlates of consciousness in the front or in the back of the cerebral cortex? Clinical and neuroimaging evidence. *Journal of Neuroscience*, *37*, 9603–9613. https://doi.org/10.1523/JNEUROSCI.3218-16 .2017, PubMed: 28978697
- Bruchmann, M., Mertens, L., Schindler, S., & Straube, T. (2023). Potentiated early neural responses to fearful faces are not driven by specific face parts. *Scientific Reports*, *13*, 4613. https://doi.org/10.1038/s41598-023-31752-z, PubMed: 36944705
- Buffalo, E. A., Fries, P., Landman, R., Liang, H., & Desimone, R. (2010). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences, U.S.A.*, 107, 361–365. https://doi.org/10.1073/pnas .0907658106, PubMed: 20007766
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28. https://doi.org/10.18637/jss.v080.i01
- Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *3*63, 345–357. https://doi.org/10.1038/363345a0, PubMed: 8497317
- Cohen, M. A., Cavanagh, P., Chun, M. M., & Nakayama, K. (2012). The attentional requirements of consciousness. *Trends in Cognitive Sciences*, 16, 411–417. https://doi.org/10 .1016/j.tics.2012.06.013, PubMed: 22795561
- Cohen, M. A., Ortego, K., Kyroudis, A., & Pitts, M. (2020). Distinguishing the neural correlates of perceptual awareness and postperceptual processing. *Journal of Neuroscience*, 40, 4925–4935. https://doi.org/10.1523/JNEUROSCI.0120-20 .2020, PubMed: 32409620

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. *Journal of Neuroscience*, 11, 2383–2402. https://doi.org/10 .1523/JNEUROSCI.11-08-02383.1991, PubMed: 1869921

Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6, 119–126. https://doi.org/10.1038 /nn0203-119, PubMed: 12555104

de Graaf, T. A., Hsieh, P.-J., & Sack, A. T. (2012). The 'correlates' in neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*, 191–197. https://doi.org/10.1016/j .neubiorev.2011.05.012, PubMed: 21651927

Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*, 200–227. https://doi.org/10.1016/j.neuron.2011.03.018, PubMed: 21521609

Dellert, T., Krebs, S., Bruchmann, M., Schindler, S., Peters, A., & Straube, T. (2022). Neural correlates of consciousness in an attentional blink paradigm with uncertain target relevance. *Neuroimage*, 264, 119679. https://doi.org/10.1016 /j.neuroimage.2022.119679, PubMed: 36220535

Dellert, T., Müller-Bardorff, M., Schlossmacher, I., Pitts, M., Hofmann, D., Bruchmann, M., et al. (2021). Dissociating the neural correlates of consciousness and task relevance in face perception using simultaneous EEG-fMRI. *Journal* of Neuroscience, 41, 7864–7875. https://doi.org/10.1523 /JNEUROSCI.2799-20.2021, PubMed: 34301829

Dembski, C., Koch, C., & Pitts, M. (2021). Perceptual awareness negativity: A physiological correlate of sensory consciousness. *Trends in Cognitive Sciences*, 25, 660–670. https://doi.org/10.1016/j.tics.2021.05.009, PubMed: 34172384

Derda, M., Koculak, M., Windey, B., Gociewicz, K., Wierzchoń, M., Cleeremans, A., et al. (2019). The role of levels of processing in disentangling the ERP signatures of conscious visual processing. *Consciousness and Cognition*, 73, 102767. https://doi.org/10.1016/j.concog.2019.102767, PubMed: 31260842

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222. https://doi.org/10.1146/annurev.ne.18.030195 .001205, PubMed: 7605061

Di Russo, F., Martínez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, 13, 486–499. https://doi.org/10 .1093/cercor/13.5.486, PubMed: 12679295

Doradzińska, Ł., & Bola, M. (2023). I focus only when I see your fear—Fearful faces are not prioritized by attention when processed outside of awareness. *Cerebral Cortex*, 33, 9233–9249. https://doi.org/10.1093/cercor/bhad194, PubMed: 37339886

Doradzińska, Ł., Wójcik, M. J., Paź, M., Nowicka, M. M., Nowicka, A., & Bola, M. (2020). Unconscious perception of one's own name modulates amplitude of the P3B ERP component. *Neuropsychologia*, 147, 107564. https://doi.org /10.1016/j.neuropsychologia.2020.107564, PubMed: 32707162

Dykstra, A. R., Halgren, E., Gutschalk, A., Eskandar, E. N., & Cash, S. S. (2016). Neural correlates of auditory perceptual awareness and release from informational masking recorded directly from human cortex: A case study. *Frontiers in Neuroscience*, 10, 472. https://doi.org/10.3389/fnins.2016 .00472, PubMed: 27812318

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234. https://doi.org/10.1016/0013 -4694(96)95711-9, PubMed: 8862112 Eiserbeck, A., Enge, A., Rabovsky, M., & Abdel Rahman, R. (2022). Electrophysiological chronometry of graded consciousness during the attentional blink. *Cerebral Cortex*, *32*, 1244–1259. https://doi.org/10.1093/cercor/bhab289, PubMed: 34435621

Eklund, R., Gerdfeldter, B., & Wiens, S. (2019). Effects of a manual response requirement on early and late correlates of auditory awareness. *Frontiers in Psychology*, 10, 2083. https://doi.org/10.3389/fpsyg.2019.02083, PubMed: 31551899

Eklund, R., Gerdfeldter, B., & Wiens, S. (2020). Is auditory awareness negativity confounded by performance? *Consciousness and Cognition*, *83*, 102954. https://doi.org/10 .1016/j.concog.2020.102954, PubMed: 32485343

Eklund, R., & Wiens, S. (2018). Visual awareness negativity is an early neural correlate of awareness: A preregistered study with two Gabor sizes. *Cognitive, Affective, & Behavioral Neuroscience, 18*, 176–188. https://doi.org/10.3758/s13415 -018-0562-z, PubMed: 29344763

Eklund, R., & Wiens, S. (2019). Auditory awareness negativity is an electrophysiological correlate of awareness in an auditory threshold task. *Consciousness and Cognition*, 71, 70–78. https://doi.org/10.1016/j.concog.2019.03.008, PubMed: 30928900

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2007). Masking disrupts reentrant processing in human visual cortex. *Journal of Cognitive Neuroscience*, *19*, 1488–1497. https://doi.org/10.1162/jocn.2007.19.9.1488, PubMed: 17714010

Förster, J., Koivisto, M., & Revonsuo, A. (2020). ERP and MEG correlates of visual consciousness: The second decade. *Consciousness and Cognition*, 80, 102917. https://doi.org/10 .1016/j.concog.2020.102917, PubMed: 32193077

Fries, P. (2015). Rhythms for cognition: Communication through coherence. *Neuron*, 88, 220–235. https://doi.org/10 .1016/j.neuron.2015.09.034, PubMed: 26447583

Fries, P., Womelsdorf, T., Oostenveld, R., & Desimone, R. (2008). The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4. *Journal of Neuroscience*, 28, 4823–4835. https://doi.org/10.1523/JNEUROSCI.4499-07.2008, PubMed: 18448659

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., et al. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience*, 7, 267. https://doi.org/10.3389/fnins.2013.00267, PubMed: 24431986

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., et al. (2014). MNE software for processing MEG and EEG data. *Neuroimage*, *86*, 446–460. https://doi.org/10.1016/j.neuroimage.2013.10.027, PubMed: 24161808

Gray, K. L. H., Adams, W. J., Hedger, N., Newton, K. E., & Garner, M. (2013). Faces and awareness: Low-level, not emotional factors determine perceptual dominance. *Emotion*, 13, 537–544. https://doi.org/10.1037/a0031403, PubMed: 23398580

Graziano, M. S. A. (2022). A conceptual framework for consciousness. *Proceedings of the National Academy of Sciences, U.S.A.*, *119*, e2116933119. https://doi.org/10.1073 /pnas.2116933119, PubMed: 35486693

Gutschalk, A., Micheyl, C., & Oxenham, A. J. (2008). Neural correlates of auditory perceptual awareness under informational masking. *PLoS Biology*, *6*, e138. https://doi.org /10.1371/journal.pbio.0060138, PubMed: 18547141

Harter, M. R., & Aine, C. J. (1984). Brain mechanisms of visual selective attention. In R. Parasuraman & D. R. Davies (Eds.), *Varieties of attention* (pp. 293–321). New York: Academic Press. Hautus, M. J. (1995). Corrections for extreme proportions and their biasing effects on estimated values of d'. *Behavior Research Methods, Instruments, & Computers, 27*, 46–51. https://doi.org/10.3758/BF03203619

Hedger, N., Adams, W. J., & Garner, M. (2015). Fearful faces have a sensory advantage in the competition for awareness. *Journal of Experimental Psychology: Human Perception and Performance*, *41*, 1748–1757. https://doi.org/10.1037 /xhp0000127, PubMed: 26280260

Hedger, N., Garner, M., & Adams, W. J. (2019). Do emotional faces capture attention, and does this depend on awareness? Evidence from the visual probe paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, 45, 790–802. https://doi.org/10.1037 /xhp0000640, PubMed: 30998068

Hedger, N., Gray, K. L. H., Garner, M., & Adams, W. J. (2016). Are visual threats prioritized without awareness? A critical review and meta-analysis involving 3 behavioral paradigms and 2696 observers. *Psychological Bulletin*, *142*, 934–968. https://doi.org/10.1037/bul0000054, PubMed: 27123863

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., et al. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, *372*, 543–546. https://doi.org/10.1038 /372543a0, PubMed: 7990926

Hillyard, S. A. (1993). Electrical and magnetic brain recordings: Contributions to cognitive neuroscience. *Current Opinion in Neurobiology*, *3*, 217–224. https://doi.org/10.1016/0959 -4388(93)90213-I, PubMed: 8513235

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences, U.S.A.*, 95, 781–787. https://doi.org/10.1073/pnas.95.3.781, PubMed: 9448241

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70. https://www.jstor.org/stable/4615733

Hutchinson, B. T. (2019). Toward a theory of consciousness: A review of the neural correlates of inattentional blindness. *Neuroscience & Biobebavioral Reviews*, *104*, 87–99. https://doi.org/10.1016/j.neubiorev.2019.06.003, PubMed: 31173773

Hutchinson, B. T., Pammer, K., Bandara, K., & Jack, B. N. (2022). A tale of two theories: A meta-analysis of the attention set and load theories of inattentional blindness. *Psychological Bulletin*, 148, 370–396. https://doi.org/10.1037 /bul0000371

Jas, M., Engemann, D. A., Bekhti, Y., Raimondo, F., & Gramfort, A. (2017). Autoreject: Automated artifact rejection for MEG and EEG data. *Neuroimage*, 159, 417–429. https://doi.org/10 .1016/j.neuroimage.2017.06.030, PubMed: 28645840

Jas, M., Engemann, D., Raimondo, F., Bekhti, Y., & Gramfort, A. (2016). Automated rejection and repair of bad trials in MEG/ EEG. 2016 International Workshop on Pattern Recognition in Neuroimaging (PRNI), 1–4. https://doi.org/10.1109/PRNI .2016.7552336

JASP Team. (2021). JASP (0.15) [Computer software]. https://jasp-stats.org/

Junghöfer, M., Bradley, M. M., Elbert, T. R., & Lang, P. J. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, *38*, 175–178. https://doi.org/10.1111/1469 -8986.3820175, PubMed: 11347862

Kappenman, E. S., Farrens, J. L., Luck, S. J., & Proudfit, G. H. (2014). Behavioral and ERP measures of attentional bias to threat in the dot-probe task: Poor reliability and lack of correlation with anxiety. *Frontiers in Psychology*, *5*, 1368. https://doi.org/10.3389/fpsyg.2014.01368, PubMed: 25538644 Kastner, S., Pinsk, M. A., Weerd, P. D., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22, 751–761. https://doi.org/10.1016 /S0896-6273(00)80734-5, PubMed: 10230795

Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*, 1263–1276. https://doi.org/10.1016 /S0028-3932(01)00116-6, PubMed: 11566310

Keil, A., Debener, S., Gratton, G., Junghöfer, M., Kappenman, E. S., Luck, S. J., et al. (2014). Committee report: Publication guidelines and recommendations for studies using electroencephalography and magnetoencephalography. *Psychophysiology*, *51*, 1–21. https://doi.org/10.1111/psyp .12147, PubMed: 24147581

Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: Progress and problems. *Nature Reviews Neuroscience*, *17*, 307–321. https://doi.org/10.1038 /nrn.2016.22, PubMed: 27094080

Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, *11*, 16–22. https://doi.org/10.1016/j.tics.2006.10.012, PubMed: 17129748

Koivisto, M., & Grassini, S. (2016). Neural processing around 200 ms after stimulus-onset correlates with subjective visual awareness. *Neuropsychologia*, 84, 235–243. https://doi.org /10.1016/j.neuropsychologia.2016.02.024, PubMed: 26944872

Koivisto, M., Grassini, S., Salminen-Vaparanta, N., & Revonsuo, A. (2017). Different electrophysiological correlates of visual awareness for detection and identification. *Journal of Cognitive Neuroscience*, 29, 1621–1631. https://doi.org/10 .1162/jocn a 01149, PubMed: 28557691

Koivisto, M., Kainulainen, P., & Revonsuo, A. (2009). The relationship between awareness and attention: Evidence from ERP responses. *Neuropsychologia*, 47, 2891–2899. https://doi.org/10.1016/j.neuropsychologia.2009.06.016, PubMed: 19545577

Koivisto, M., Lähteenmäki, M., Sørensen, T. A., Vangkilde, S., Overgaard, M., & Revonsuo, A. (2008). The earliest electrophysiological correlate of visual awareness? *Brain and Cognition*, 66, 91–103. https://doi.org/10.1016/j.bandc.2007 .05.010, PubMed: 17664036

Koivisto, M., & Revonsuo, A. (2007). Electrophysiological correlates of visual consciousness and selective attention. *NeuroReport*, 18, 753–756. https://doi.org/10.1097/WNR .0b013e3280c143c8, PubMed: 17471060

Koivisto, M., & Revonsuo, A. (2008). The role of selective attention in visual awareness of stimulus features: Electrophysiological studies. *Cognitive, Affective, & Behavioral Neuroscience*, 8, 195–210. https://doi.org/10.3758/CABN.8.2.195, PubMed: 18589509

Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience & Biobehavioral Reviews*, 34, 922–934. https://doi.org/10.1016/j .neubiorev.2009.12.002, PubMed: 20005249

Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006).
Independence of visual awareness from the scope of attention: An electrophysiological study. *Cerebral Cortex*, *16*, 415–424. https://doi.org/10.1093/cercor/bhi121, PubMed: 15958780

Koivisto, M., Revonsuo, A., & Salminen, N. (2005). Independence of visual awareness from attention at early processing stages. *NeuroReport*, *16*, 817–821. https://doi.org /10.1097/00001756-200505310-00008, PubMed: 15891577

Koivisto, M., Salminen-Vaparanta, N., Grassini, S., & Revonsuo, A. (2016). Subjective visual awareness emerges prior to P3. *European Journal of Neuroscience*, 43, 1601–1611. https:// doi.org/10.1111/ejn.13264, PubMed: 27109009 Kronemer, S. I., Aksen, M., Ding, J. Z., Ryu, J. H., Xin, Q., Ding, Z., et al. (2022). Human visual consciousness involves large scale cortical and subcortical networks independent of task report and eye movement activity. *Nature Communications*, *13*, 7342. https://doi.org/10.1038/s41467-022-35117-4, PubMed: 36446792

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). ImerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26. https://doi.org/10 .18637/jss.v082.i13

Lamme, V. A. F. (2000). Neural mechanisms of visual awareness: A linking proposition. *Brain and Mind*, 1, 385–406. https:// doi.org/10.1023/A:1011569019782

Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7, 12–18. https://doi.org/10.1016/S1364-6613(02)00013-X, PubMed: 12517353

Lamme, V. A. F. (2004). Separate neural definitions of visual consciousness and visual attention; A case for phenomenal awareness. *Neural Networks*, 17, 861–872. https://doi.org/10 .1016/j.neunet.2004.02.005, PubMed: 15288903

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, 10, 494–501. https://doi.org/10.1016/j.tics.2006.09.001, PubMed: 16997611

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, 1, 204–220. https://doi.org/10.1080/17588921003731586, PubMed: 24168336

Lamme, V. A. F. (2018). Challenges for theories of consciousness: Seeing or knowing, the missing ingredient and how to deal with panpsychism. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 373, 20170344. https://doi.org/10.1098 /rstb.2017.0344, PubMed: 30061458

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23, 571–579. https://doi.org/10 .1016/S0166-2236(00)01657-X, PubMed: 11074267

Langeslag, S. J. E., & van Strien, J. W. (2018). Early visual processing of snakes and angry faces: An ERP study. *Brain Research*, 1678, 297–303. https://doi.org/10.1016/j.brainres .2017.10.031, PubMed: 29102778

Lenth, R. (2024). *Emmeans: Estimated marginal means, aka least-squares means* (1.4.7.2020) [Computer software].

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, timing, timing: Fast decoding of object information from intracranial field potentials in human visual cortex. *Neuron*, *62*, 281–290. https://doi.org/10.1016/j.neuron.2009.02.025, PubMed: 19409272

Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In E. S. Kappenman & S. J. Luck (Eds.), *The Oxford handbook of event-related potential components* (pp. 330–360). Oxford University Press. https:// doi.org/10.1093/oxfordhb/9780195374148.013.0161

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, *33*, 64–87. https:// doi.org/10.1006/cogp.1997.0660, PubMed: 9212722

Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308. https://doi.org/10.1111/j.1469 -8986.1994.tb02218.x, PubMed: 8008793

Luck, S. J., & Kappenman, E. S. (2012). The Oxford handbook of event-related potential components. Oxford University Press.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, 4, 432–440. https://doi.org/10.1016/S1364-6613(00)01545-X, PubMed: 11058821

Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods*, 49, 1494–1502. https://doi.org/10.3758/s13428-016-0809-y, PubMed: 27620283

Mado Proverbio, A., & Zani, A. (2003). Time course of brain activation during graphemic/phonologic processing in reading: An ERP study. *Brain and Language*, *87*, 412–420. https://doi.org/10.1016/S0093-934X(03)00139-1, PubMed: 14642543

Maier, A., & Tsuchiya, N. (2021). Growing evidence for separate neural mechanisms for attention and consciousness. *Attention, Perception, & Psychophysics*, 83, 558–576. https://doi.org/10.3758/s13414-020-02146-4, PubMed: 33034851

Makeig, S., Jung, T.-P., Ghahremani, D., & Sejnowski, T. J. (1996). *Independent component analysis of simulated ERP data*. Institute for Neural Computation, University of California: Technical Report INC-9606.

Maunsell, J. H. R., & Cook, E. P. (2002). The role of attention in visual processing. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 357, 1063–1072. https://doi.org/10.1098/rstb.2002.1107, PubMed: 12217174

McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience*, 19, 431–441. https://doi.org/10.1523/JNEUROSCI.19-01-00431.1999, PubMed: 9870971

Meyer, K. (2011). Primary sensory cortices, top–down projections and conscious experience. *Progress in Neurobiology*, *94*, 408–417. https://doi.org/10.1016/j pneurobio.2011.05.010, PubMed: 21683755

Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual Review of Psychology*, 68, 47–72. https://doi.org/10.1146/annurev-psych-122414-033400, PubMed: 28051934

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229, 782–784. https://doi.org/10.1126/science.4023713, PubMed: 4023713

Mudrik, L., & Deouell, L. Y. (2022). Neuroscientific evidence for processing without awareness. *Annual Review of Neuroscience*, 45, 403–423. https://doi.org/10.1146/annurev -neuro-110920-033151, PubMed: 35803585

Noudoost, B., Chang, M. H., Steinmetz, N. A., & Moore, T. (2010). Top–down control of visual attention. *Current Opinion in Neurobiology*, 20, 183–190. https://doi.org/10 .1016/j.conb.2010.02.003, PubMed: 20303256

O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24, 939–973. https://doi.org/10.1017 /S0140525X01000115, PubMed: 12239892

Ojanen, V., Revonsuo, A., & Sams, M. (2003). Visual awareness of low-contrast stimuli is reflected in event-related brain potentials. *Psychophysiology*, *40*, 192–197. https://doi.org/10 .1111/1469-8986.00021, PubMed: 12820860

Olson, I. R., Chun, M. M., & Allison, T. (2001). Contextual guidance of attention: Human intracranial event-related potential evidence for feedback modulation in anatomically early temporally late stages of visual processing. *Brain*, *124*, 1417–1425. https://doi.org/10.1093/brain/124.7.1417, PubMed: 11408336

Pegna, A. J., Darque, A., Berrut, C., & Khateb, A. (2011). Early ERP modulation for task-irrelevant subliminal faces. *Frontiers in Psychology*, 2, 88. https://doi.org/10.3389/fpsyg.2011 .00088, PubMed: 21687457 Pegna, A. J., Landis, T., & Khateb, A. (2008). Electrophysiological evidence for early non-conscious processing of fearful facial expressions. *International Journal of Psychophysiology*, 70, 127–136. https://doi.org/10.1016/j.ijpsycho.2008.08.007, PubMed: 18804496

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: From modulation of sensory processing to top–down control. *Journal of Neuroscience*, 23, 3990–3998. https://doi.org/10.1523 /JNEUROSCI.23-10-03990.2003, PubMed: 12764083

Pins, D., & Ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral Cortex*, 13, 461–474. https://doi .org/10.1093/cercor/13.5.461, PubMed: 12679293

Pitts, M. A., Martínez, A., & Hillyard, S. A. (2010). When and where is binocular rivalry resolved in the visual cortex? *Journal of Vision*, *10*, 25. https://doi.org/10.1167/10.14.25, PubMed: 21191137

Pitts, M. A., Martínez, A., & Hillyard, S. A. (2012). Visual processing of contour patterns under conditions of inattentional blindness. *Journal of Cognitive Neuroscience*, 24, 287–303. https://doi .org/10.1162/jocn a 00111, PubMed: 21812561

Pitts, M. A., Metzler, S., & Hillyard, S. A. (2014). Isolating neural correlates of conscious perception from neural correlates of reporting one's perception. *Frontiers in Psychology*, *5*, 1078. https://doi.org/10.3389/fpsyg.2014 .01078, PubMed: 25339922

Pitts, M. A., Padwal, J., Fennelly, D., Martínez, A., & Hillyard, S. A. (2014). Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *Neuroimage*, 101, 337–350. https://doi.org/10.1016/j .neuroimage.2014.07.024, PubMed: 25063731

Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2006). Neural systems for orienting attention to the location of threat signals: An event-related fMRI study. *Neuroimage*, *31*, 920–933. https://doi.org/10.1016/j .neuroimage.2005.12.034. PubMed: 16487729

Qiu, Z., Becker, S. I., & Pegna, A. J. (2022a). Spatial attention shifting to emotional faces is contingent on awareness and task relevancy. *Cortex*, 151, 30–48. https://doi.org/10.1016/j .cortex.2022.02.009, PubMed: 35390549

Qiu, Z., Becker, S. I., & Pegna, A. J. (2022b). Spatial attention shifting to fearful faces depends on visual awareness in attentional blink: An ERP study. *Neuropsychologia*, *172*, 108283. https://doi.org/10.1016/j.neuropsychologia.2022 .108283, PubMed: 35661782

R Core Team. (2021). R: A language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition*, 20, 972–983. https://doi.org /10.1016/j.concog.2011.03.019, PubMed: 21482150

Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, *3*, 1–23. https://doi.org/10.1023/B:PHEN .0000041900.30172.e8

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, 27, 611–647. https://doi.org/10.1146/annurev.neuro.26.041002 .131039, PubMed: 15217345

Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, *26*, 703–714. https://doi.org/10.1016/S0896-6273(00)81206-4, PubMed: 10896165

RStudio Team. (2021). *RStudio: Integrated development environment for R [Computer software]*. RStudio, PBC. https://www.rstudio.com/ Rutiku, R., & Bachmann, T. (2017). Juxtaposing the real-time unfolding of subjective experience and ERP neuromarker dynamics. *Consciousness and Cognition*, *54*, 3–19. https:// doi.org/10.1016/j.concog.2017.05.003, PubMed: 28554797

Satterthwaite, F. E. (1941). Synthesis of variance. *Psychometrika*, 6, 309–316. https://doi.org/10.1007/BF02288586

Schelonka, K., Graulty, C., Canseco-Gonzalez, E., & Pitts, M. A. (2017). ERP signatures of conscious and unconscious word and letter perception in an inattentional blindness paradigm. *Consciousness and Cognition*, 54, 56–71. https://doi.org/10 .1016/j.concog.2017.04.009, PubMed: 28506434

Schlossmacher, I., Dellert, T., Bruchmann, M., & Straube, T. (2021). Dissociating neural correlates of consciousness and task relevance during auditory processing. *Neuroimage*, 228, 117712. https://doi.org/10.1016/j.neuroimage.2020.117712, PubMed: 33387630

Schlossmacher, I., Dellert, T., Pitts, M., Bruchmann, M., & Straube, T. (2020). Differential effects of awareness and task relevance on early and late ERPs in a no-report visual oddball paradigm. *Journal of Neuroscience*, 40, 2906–2913. https://doi.org/10.1523/jneurosci.2077-19.2020, PubMed: 32122954

Schröder, P., Nierhaus, T., & Blankenburg, F. (2021). Dissociating perceptual awareness and postperceptual processing: The P300 is not a reliable marker of somatosensory target detection. *Journal of Neuroscience*, 41, 4686–4696. https://doi.org/10.1523/JNEUROSCI.2950-20 .2021, PubMed: 33849946

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology*, *41*, 441–449. https://doi.org/10.1111/j.1469-8986.2004.00174.x, PubMed: 15102130

Sergent, C., Corazzol, M., Labouret, G., Stockart, F., Wexler, M., King, J.-R., et al. (2021). Bifurcation in brain dynamics reveals a signature of conscious processing independent of report. *Nature Communications*, *12*, 1149. https://doi.org/10.1038 /s41467-021-21393-z, PubMed: 33608533

Shafto, J. P., & Pitts, M. A. (2015). Neural signatures of conscious face perception in an inattentional blindness paradigm. *Journal of Neuroscience*, 35, 10940–10948. https://doi.org/10.1523/JNEUROSCI.0145-15.2015, PubMed: 26245958

Silverstein, B. H., Snodgrass, M., Shevrin, H., & Kushwaha, R. (2015). P3b, consciousness, and complex unconscious processing. *Cortex*, 73, 216–227. https://doi.org/10.1016/j .cortex.2015.09.004, PubMed: 26474391

Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception*, 28, 1059–1074. https://doi.org/10.1068/p281059, PubMed: 10694957

Snyder, J. S., Yerkes, B. D., & Pitts, M. A. (2015). Testing domain-general theories of perceptual awareness with auditory brain responses. *Trends in Cognitive Sciences*, 19, 295–297. https://doi.org/10.1016/j.tics.2015.04.002 25960421

Stan Development Team. 2024. Stan modeling language users guide and reference manual, 2.34. https://mc-stan.org

Sun, B., Zeng, X., Chen, X., Zhao, J., & Fu, S. (2023). Neural correlates of conscious processing of emotional faces: Evidence from event-related potentials. *Neuropsychologia*, *182*, 108478. https://doi.org/10.1016/j.neuropsychologia.2023 .108478, PubMed: 36707025

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., et al. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, 168, 242–249. https://doi.org/10.1016/j .psychres.2008.05.006, PubMed: 19564050

- Travis, S. L., Dux, P. E., & Mattingley, J. B. (2019). Neural correlates of goal-directed enhancement and suppression of visual stimuli in the absence of conscious perception. *Attention, Perception, & Psychophysics*, 81, 1346–1364. https://doi.org/10.3758/s13414-018-1615-7, PubMed: 30378084
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432. https://doi .org/10.1007/s11222-016-9696-4
- Veser, S., O'Shea, R. P., Schröger, E., Trujillo-Barreto, N. J., & Roeber, U. (2008). Early correlates of visual awareness following orientation and colour rivalry. *Vision Research*, 48, 2359–2369. https://doi.org/10.1016/j.visres.2008.07.024, PubMed: 18727933
- Wickens, T. D. (2001). Elementary signal detection theory. Oxford University Press. https://doi.org/10.1093/acprof:oso /9780195092509.001.0001
- Widmann, A., Schröger, E., & Maess, B. (2015). Digital filter design for electrophysiological data—A practical approach. *Journal of Neuroscience Methods*, 250, 34–46. https://doi.org /10.1016/j.jneumeth.2014.08.002, PubMed: 25128257

uncorrected

- Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods*, 42, 671–684. https://doi.org/10.3758/BRM.42.3.671, PubMed: 20805589
- Womelsdorf, T., & Fries, P. (2007). The role of neuronal synchronization in selective attention. *Current Opinion in Neurobiology*, 17, 154–160. https://doi.org/10.1016/j.conb .2007.02.002, PubMed: 17306527
- Wójcik, M. J., Nowicka, M. M., Bola, M., & Nowicka, A. (2019). Unconscious detection of one's own image.
 Psychological Science, *30*, 471–480. https://doi.org/10.1177 /0956797618822971, PubMed: 30785866
- Yaron, I., Melloni, L., Pitts, M., & Mudrik, L. (2022). The ConTraSt database for analysing and comparing empirical studies of consciousness theories. *Nature Human Behaviour*, 6, 593–604. https://doi.org/10.1038/s41562-021 -01284-5, PubMed: 35190711
- Zotto, M. D., & Pegna, A. J. (2015). Processing of masked and unmasked emotional faces under different attentional conditions: An electrophysiological investigation. *Frontiers in Psychology*, 6, 1691. https://doi.org/10.3389/fpsyg.2015 .01691, PubMed: 26583003

28 Journal of Cognitive Neuroscience

List of author's publications

- 1. **Doradzińska, L.**, & Bola, M. (in press). Early electrophysiological correlates of perceptual consciousness are affected by both exogenous and endogenous attention. *Journal of Cognitive Neuroscience*. *
- 2. **Doradzińska, L.**, & Bola, M. (2023). I focus only when I see your fear—fearful faces are not prioritized by attention when processed outside of awareness. *Cerebral Cortex*, 33(15), 9233-9249. *
- Rutkowska, N., Doradzińska, L., & Bola, M. (2022). Attentional Prioritization of Complex, Naturalistic Stimuli Maintained in Working-Memory–A Dot-Probe Event-Related Potentials Study. *Frontiers in Human Neuroscience*, 16, 838338.
- Doradzińska, Ł., Furtak, M., & Bola, M. (2022). Perception of semantic relations in scenes: A registered report study of attention hold. *Consciousness and Cognition*, 100, 103315. *
- 5. Bola, M., & **Doradzińska**, L. (2021). Perceptual awareness negativity—does it reflect awareness or attention?. *Frontiers in Human Neuroscience*, *15*, 742513.
- 6. Bola, M., Paź, M., **Doradzińska, L.**, & Nowicka, A. (2021). The self-face captures attention without consciousness: Evidence from the N2pc ERP component analysis. *Psychophysiology*, *58*(4), e13759.
- Doradzińska, Ł., Wójcik, M. J., Paź, M., Nowicka, M. M., Nowicka, A., & Bola, M. (2020). Unconscious perception of one's own name modulates amplitude of the P3B ERP component. *Neuropsychologia*, 147, 107564.
- Furtak, M., Doradzińska, Ł., Ptashynska, A., Mudrik, L., Nowicka, A., & Bola, M. (2020). Automatic attention capture by threatening, but not by semantically incongruent natural scene images. *Cerebral Cortex*, 30(7), 4158-4168.
- * Publications constituting the present dissertation