Unmasking the perception of temporal successions: bridge building between metacontrast masking and temporal integration and segregation processes

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Foreword

The journey of this PhD began in a dark room that was only illuminated by the bright screen of a CRT monitor. I was participating in a psychophysical experiment; my head was placed in a headrest and my eyes were focused on a small fixation cross in the middle of the screen. My task was to watch a sequence of two visual stimuli that were presented right on the fixation cross and I had to report on the shape of the first one. While the first visual stimulus, called the target, was a square or diamond shape that was completely filled with black color, the second stimulus, called the mask, was a larger version of the superimposed targets but its interior was empty so that each target could fit snuggly inside of it. While the white light of the screen's background slowly started to burn my eyes, I started to question my common sense. Even after half an hour and dozens of trials I had not seen the target once. For me, each trial consisted of the presentation of the mask and the target was completely absent; just as if it was not presented at all. Was there an error in the experiment?

I have always been a very conscientious participant in experiments and at that time I nearly decided to abort the experiment prematurely since - at least in my opinion - my data would not be good for anything. The only thing that I did was guessing the shape of the target without ever getting a hint of it. I was nearly at the point of standing up and leaving the room, when I started to see a blackish hue that was only just slightly more than nothing but could not have been the mask. Although there were still enough trials in which I could not see the target at all, I started to pick up more and more visual information of the target. Sometimes I could only see one edge or one corner of it, sometimes a full-fletched target but varying in its contrast. However, although I could now see something of the target, I still kept questioning my common sense. Though the presentation of the target-mask sequence does not appear to elicit an especially rich visual experience, I started to perceive a wide range of strange things, like the target and mask rotating towards each other or a simultaneous perception of the target inside of the mask although they are never presented together on the screen.

Eventually, something happened that has been deeply fascinating me until this very day: I perceived the target as a wave of contours that slowly expanded from the fixation cross and created the mask in one swift movement. I termed this percept the *opening lotus* and I could not wrap my head around the fact that such a rich and satisfactory visual percept could be created from the sparse presentation of two successive simple geometric objects. How could this be?

If I could infect you with at least a slight amount of the curiosity that I experienced back then, then I want to invite you to stay a little longer so that I can tell you about my journey into the brain and my venturing into consciousness and temporal phenomena.

Summary

Temporal and masking research share theoretical, methodological and empirical similarities indicating that they might investigate a similar aspect of our neural functioning. Nevertheless, temporal and masking mechanisms have never before been concurrently investigated which is even more surprising since each mechanism has been proposed to be relevant in the respective other field of research. The three studies of this dissertation constitute a first step towards building a bridge between the temporal and masking research. In each of our studies, we conducted a metacontrast masking experiment and asked our participants to report on each trial whether they perceived the target-mask sequence temporally integrated, temporally segregated or masked while their neural activity was continuously recorded.

By contrasting the neural activity between perceptual reports, our findings demonstrate pre-stimulus theta, alpha and beta phase differences between temporally integrated and segregated percepts. While we associated theta and alpha phase differences with a bottom-up temporal mechanism in the ventral stream, we associated beta phase differences with a top-down bias that frontal brain areas exert on brain areas further down in the neural hierarchy. In addition, post-stimulus differences in the event-related potentials indicated a spatio-temporal integration mechanism to be relevant for both temporally integrated and masked percepts. Overall, our findings extend established neural correlates of temporal mechanisms to the metacontrast masking paradigm. In addition, we demonstrate the potential information gain from concurrently investigating temporal and masking mechanisms by indicating a shared mechanism for both temporal and masking phenomena.

1. Theoretical introduction

1.1 Research on temporal mechanisms

The exposure time of a photo camera determines the amount of successive visual information that is integrated into the same photograph. A razor-sharp photograph of the stars in the night sky can be created by selecting a short exposure time while the trails of the stars can be displayed in a single photograph by selecting a long exposure time. The visual system has been proposed to act similarly to a photo camera with a relatively stable exposure time thereby creating a series of snapshots of our environment (VanRullen & Koch, 2003; VanRullen, 2016a). This analogy implicates a discrete perception of time in which successive stimuli may be erroneously fused into the same perceptual moment (Stroud,1956; Block, 2014). Such a limited temporal resolution of our visual system runs counter to our intuition of a continuous perception of time but is already hinted at in a children's toy in the 18th century. The so-called thaumatrope consists of a disk with two different images on each side (e.g. flowers on one side and an empty vase on the other side) and a pair of strings that are attached to it. By twisting and pulling on these strings, the disk starts to rotate fast and thereby creates a fused perception of both images (flowers in the vase).

Besides evidence based on a child's toy, experiments have repeatedly demonstrated the erroneous simultaneous perception of successive events. In the two-flash task (e.g. Exner, 1875; Samaha & Postle, 2015; Milton & Pleydell-Pearce, 2016; Ronconi & Melcher, 2017), two low contrast flashes are presented in quick succession at the same spot in the visual periphery and participants are asked to report whether they perceived two flashes or only one flash (figure 1c).

Findings demonstrate that the shorter the inter-stimulus interval between the flashes becomes, the more likely participants erroneously report to perceive only one flash. Other paradigms take advantage of this erroneous simultaneous perception and render a task that would normally be nearly unsolvable solvable. The missing element task (e.g. Hogben & Di Lollo, 1974; Akyürek et al., 2010; Wutz et al., 2016; Wutz et al., 2018) for example presents participants with two grids of stimuli that when superimposed reveal one grid element that is neither occupied in the first nor second grid (figure 1b). Due to the size of the grids and their short

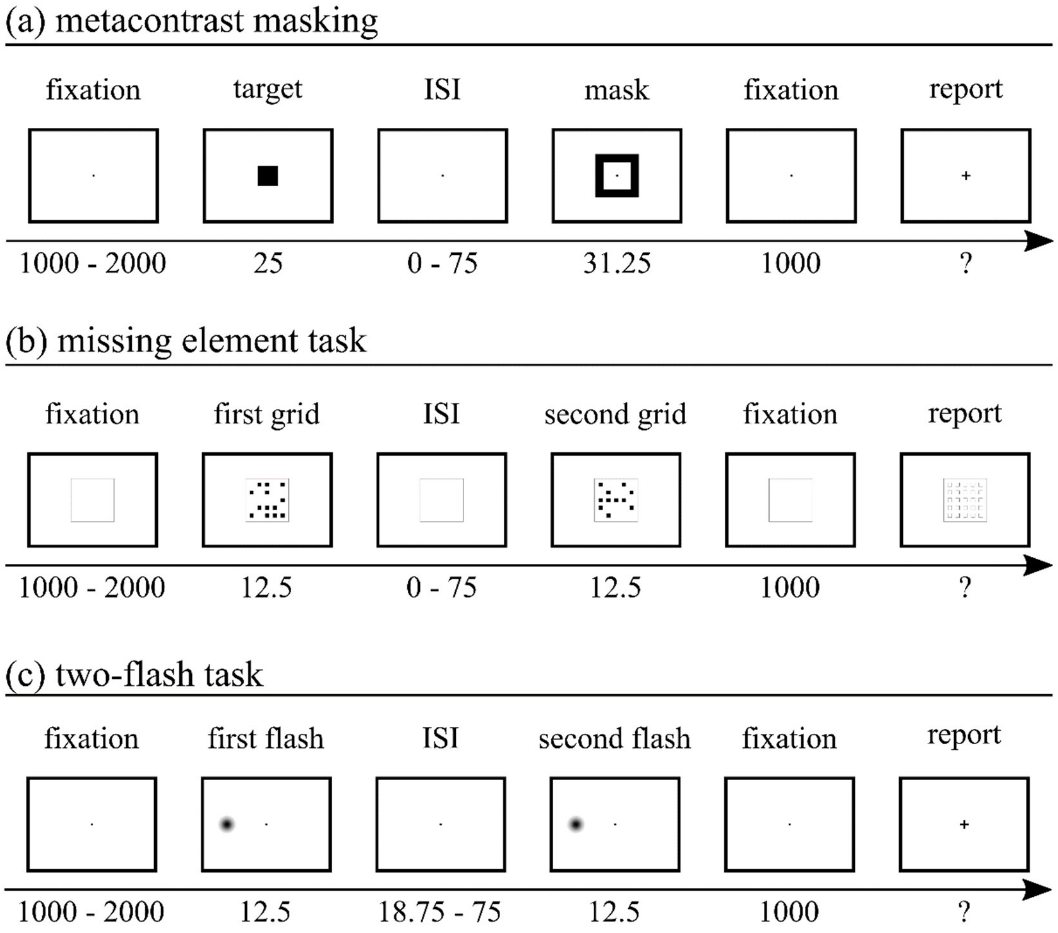

Figure 1. Illustration of each of the paradigms that will be investigated in this dissertation. Numbers under each screen correspond to their exemplified presentation duration in ms.

presentation duration, it is nearly impossible to completely memorize both of them and compare each of their grid positions in memory to identify the missing element. Nonetheless, participants identify the missing element more likely the shorter the inter-stimulus interval between the grid presentations becomes since the grids are then simultaneously perceived and the missing element pops out.

To explain the possibility for an erroneous simultaneous perception to occur, most models assume neural oscillations to be essential. Especially lower neural frequencies have been demonstrated to periodically variate the neural excitability of the underlying neural substrate thereby creating time windows of better and worse neural processing (Hanslmayr et al., 2013; Jensen et al., 2014). While neural processing is most impaired around the negative maximum of a frequency cycle, it is least impaired around the positive maximum of a frequency cycle. It has been demonstrated that a presentation of two flashes around the positive maximum of the alpha frequency cycle and hence a phase interval of better neural processing results more likely in the perception of only one flash (Varela et al., 1981). Based on this finding, the authors hypothesized that the alpha cycle produces temporal frames that either bind or parse consecutively presented stimuli. In more recent papers, the term temporal frame has been superseded by the term temporal (integration) window (see e.g. Akyürek et al., 2010; Samaha & Postle, 2015; Wutz et al., 2016; Ronconi & Melcher, 2017) but the notion behind both terms remains the same: Stimuli that are processed inside of the same temporal integration window are perceived simultaneously whereas they are perceived temporally segregated when they are processed inside of different temporal integration windows (figure 2). Models of temporal integration windows are in line with the idea of a discrete perception since each temporal integration window

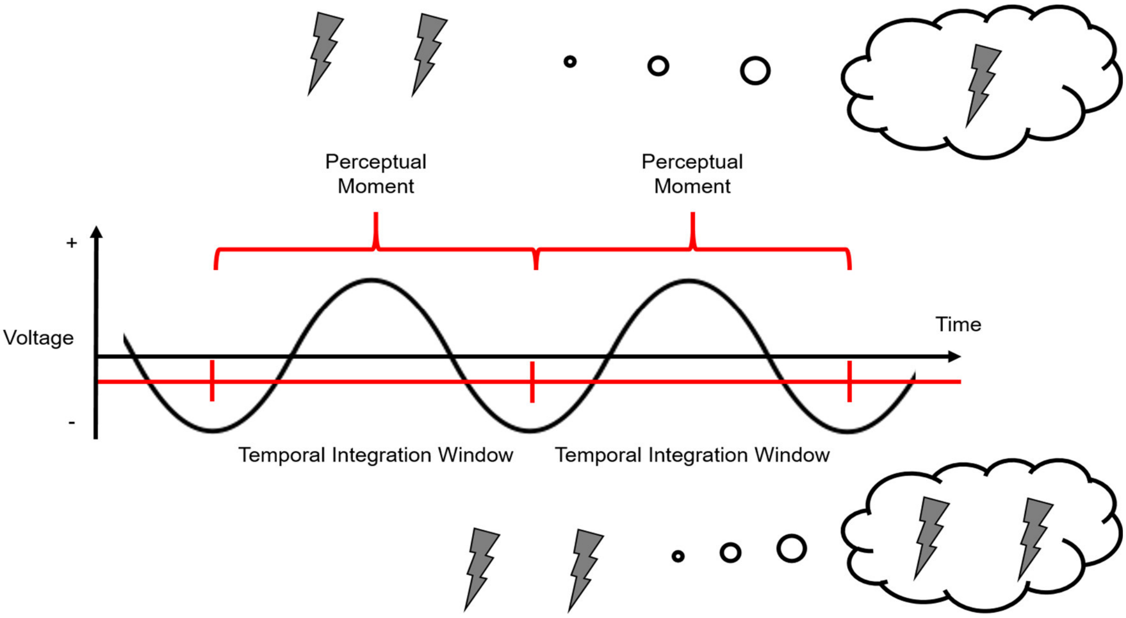

Figure 2. Illustration of a neural oscillation whose cycles might correspond to temporal integration windows. According to Varela et al. (1981) temporal integration windows may form around the positive maximum of the alpha cycle since the underlying neural substrate would be least inhibited. Temporal integration windows would be closed and reopened around the negative maximum of the alpha cycle since the underlying neural substrate would be most inhibited. The basic idea of temporal integration windows is that the same objective stimulus presentation of two successive stimuli can result in a differential temporal perception depending on whether the fall into the same or different temporal integration windows. A temporally integrated perception results from both stimuli being processed in the same temporal integration window while a temporally segregated perception results from them falling into different temporal integration windows.

would correspond to the formation of a “perceptual moment” (Stroud,1956). Despite the captivating simplicity of these models, they evoke more explanatory power than they have. Eventually, it remains unclear why stimuli tend to be perceived simultaneously when they are presented in the most excitable phase interval of a neural oscillation.

Other approaches that try to explain differences in our temporal perception refrain from the postulation of temporal integration windows and try to rely solely on the periodic variation of the neural excitability due to neural oscillations. Milton and Pleydell-Pearce (2016) propose that variations in the neural excitability affect not only the processing of each stimulus but also the processing of their inter-stimulus interval. The temporal gap between two stimuli should be neurally represented worse, if the processing of the inter-stimulus interval coincides with a phase of worse neural processing. Accordingly, an erroneous report of a simultaneous perception results from a bad representation of the successive stimulus presentation and not from a genuine simultaneous perception. Such a conclusion, however, contradicts paradigms like the missing element task that are built on the assumption that a genuine simultaneous perception is possible.

In another approach, VanRullen (2016a) proposes that the phase state that a stimulus is presented in affects its processing speed and hence the time it needs to pass the perceptual threshold. Accordingly, the subjectively perceived temporal gap between two stimuli is affected by the time that each stimulus needs to pass the perceptual threshold. If the first stimulus is presented in a less excitable phase than the second stimulus, their subjectively perceived temporal gap is shorter than their objective temporal gap. Although this approach is well suited to explain temporal perceptions that deviate from the objective stimulus presentation, it seems to be limited to near-threshold stimuli that need to pass a perceptual threshold (e.g. two-flash task). It is unclear in which way this approach would generalize to stimuli that are presented clearly above the perceptual threshold (e.g. missing element task) and whether a genuine simultaneous perception would be possible or not.

All of the presented models assume that a periodic variation of the neural excitability due to neural oscillations is key to understand temporal mechanisms. This assumption is based on an extensive amount of evidence that the pre-stimulus phase states of neural oscillations affect temporal processing (VanRullen, 2016a). Especially phase states of lower neural frequencies in the theta (3-7 Hz) and alpha (8-12 Hz) frequency range have been demonstrated to differ between correct and incorrect reports in the two-flash (Varela et al., 1981; Milton & Pleydell-Pearce, 2016; Ronconi et al., 2017) and missing element task (Wutz et al., 2016). This correlational evidence was expanded by Ronconi and Melcher (2017) with a more causal link using a sensory entrainment in a two-flash task. Sensory entrainment describes the behavior of neural oscillations to adopt the rhythmicity of a sensory stimulus that is repeatedly presented with the same frequency. After the stimulus presentation of the entrainment, the entrainment effect is still measurable for several oscillatory cycles but diminishes slowly. By manipulating the gap between the end of the entrainment and the presentation of the two flashes, the authors could precisely control the phase state of the entrained neural frequency in which the two flashes will be presented. The authors found that both an entrainment of the theta and alpha frequencies induced a behavioral oscillation of the same frequency in the performance of the two-flash task. These findings causally link the phase state of lower neural frequencies to the differential temporal perception of a stimulus sequence.

Further evidence that links temporal mechanisms to neural oscillations is provided by Samaha and Postle (2015) who demonstrated that the temporal resolution of our visual system can be predicted from the individual alpha frequency. The individual alpha frequency is a highly stable individual characteristic of our neural functioning (Grandy et al., 2013) and marks the most dominant frequency in the alpha frequency band. Under the assumption that certain phase intervals of the alpha cycle reflect temporal integration windows, the authors proposed that participants with a lower individual alpha frequency would exhibit larger temporal integration windows and vice versa. The size of the temporal integration window in turn influences the probability of two successive events to fall into the same temporal integration window which is increased for larger temporal integration windows. Accordingly, the authors demonstrated that the extent of the temporal gap between the presentations of two flashes correlated positively with the individual alpha frequency: Participants with a lower individual alpha frequency needed a longer temporal gap to reliable report two flashes than participants with a higher individual alpha frequency. Further studies have demonstrated that the most dominant frequency in the alpha frequency band can be adapted from trial to trial depending on the task demands to provide an optimal temporal processing of the upcoming stimulus presentation (Samaha et al., 2015; Wutz et al., 2018). In the framework of temporal integration windows this would translate into an adaptation of the temporal integration windows' size to increase or decrease the chance of two successive events to fall into the same temporal integration window.

Although these findings conclusively indicate the relevance of neural oscillations in temporal processing, it was questioned whether their periodic variation of the neural excitability constitutes the mechanism to influence temporal processing (Milton & Pleydell-Pearce, 2016). The authors investigated pre-stimulus phase differences in a two-flash task and additionally hypothesized that phase and power effects should interact with each other. Such an interaction would be expected if a variation of the neural excitability influences temporal processing. Accordingly, phase effects should increase with increasing power. However, no such effect could be demonstrated and has also not been reported in any other study on temporal processing. Thus, the authors suggest that phase and power effects are independent from each other and represent different aspects of our neural processing. They speculated that phase differences may hint at a fundamental periodicity in the neural communication between brain areas that affects temporal processing.

The advantage of proposing a temporal mechanism that is detached from a variation of the neural excitability renders the explanation of phase effects in higher frequency bands easier. The amplitude of the beta frequency for example is lower than that of the theta and alpha frequency band and hence its influence on the excitability of the underlying neural substrate is reduced. This, however, is irrelevant if beta phase effects reflect a fundamental information transfer in our neural system that affects temporal processing. Beta phase effects have not been demonstrated in the visual but in the auditory (Fujioka et al., 2012; Arnal et al., 2015) and somatosensory domain (Baumgarten et al., 2015). Beta power effects, however, are the only main power effects that have yet been associated with temporal processing in the visual domain (Geerligs & Akyürek, 2012). The authors conducted a missing element task and found an increased pre-stimulus beta power for trials with a correct identification of the missing element and termed this effect the integration readiness. According to the authors, an increased beta power may reflect an anticipatory top-down attentional effect that optimally prepares the visual system for the upcoming stimulus presentation.

Eventually, pre-stimulus phase and power effects are likely fundamental for the temporal processing and perception of the upcoming stimulus presentation. Whether this is the case due to a periodic variation of the neural excitability or differences in a neural communication between brain areas remains open for discussion. In addition to these pre-stimulus effects, post-stimulus ERP differences have also been associated with differences in temporal processing and perception. A more negative N1 amplitude has been demonstrated for correct reports in both the two-flash (Ronconi et al., 2017) and the missing element task (Aykürek et al., 2010). However, correct reports in the two-flash task are associated with the perception of two events while they are associated with the perception of only one event in the missing element task. Accordingly, it seems unlikely that a more negative N1 reflects the same temporal mechanism and makes it more likely that it is associated with a more general mechanism of stimulus processing that contributes to either temporal mechanism. Further ERP differences have been demonstrated for the missing element task (Akyürek et al., 2010). The authors found a more negative N2 and early P3 for correct reports that they associated with a larger engagement of spatial integration processes. In addition, they found a more positive P3 amplitude for correct reports which might indicate a reduced engagement of consolidating only one (temporally integrated) event in visual memory. It is open for discussion whether these ERP differences reflect consequences of a temporal mechanism or mark the point in time at which a temporal mechanism is executed.

To this point, I refrained from using the terms temporal integration and temporal segregation. Although these terms are widely used in the literature, they are no neutral theoretical terms but are strongly inspired by models of temporal integration windows. However, models of Milton and Pleydell-Pearce (2016) and VanRullen (2016a) would function without the postulation of a temporal integration or segregation mechanism. Eventually, I will not be able to maintain a neutral theoretical language for the remainder of this dissertation since it is built to a large extent on literature that was inspired by temporal integration windows and the notion that a genuine simultaneous perception of two successively presented stimuli is possible. Please keep in mind that despite the popularity of this model, there are alternatives to it.

However, I do not want to implicate any relation between temporal integration and segregation by using these terms. In many papers, temporal integration and segregation are at least implicitly described as the antagonistic expressions of the same underlying mechanism: two successive stimuli are either temporally integrated or temporally segregated and hence a failed temporal integration automatically implies a successful temporal segregation and vice versa (see e.g. Akyürek et al., 2010; Samaha & Postle, 2015; Ronconi et al., 2017 or Sharp et al., 2018). This assumption of a temporal antagonism, is likely inspired by models of temporal integration windows that only allow for two successive stimuli to fall into the same or different temporal integration windows but nothing in between. However, such a temporal antagonism has never been directly investigated. By shifting away from the implications of models of temporal integration windows, temporal integration and segregation mechanisms may also be independent from each other and for example be realized in disjoint temporal frequencies. Such an independence would allow for the concurrent success and failure of both mechanisms acting upon the same stimulus presentation. While the resulting percept of a concurrent success is still imaginable, a concurrent failure seems odd at first sight. This possibility, however, opened up a way to suggest an explanation for a perceptual phenomenon that even after more than 100 years of its first description (see e.g. Breitmeyer & Ögmen, 2006) remains still unexplained: the masking phenomenon.

1.2 Research on masking mechanisms

Masking in general describes a stimulus' reduction in visibility due to the presentation of another stimulus (for an overview see Breitmeyer & Ögmen, 2000, 2006). Since most of the tasks in masking paradigms are directed at the stimulus whose visibility is reduced, it is called the target while the stimulus that reduces the visibility is called the mask. While the mask is presented before the target in forward masking paradigms, the mask is presented after the target in backward masking paradigms. Backward masking phenomena question our intuition of a direct and veridical sensory access to our environment and run counter to our intuition of a continuous perception in which later events should not affect the perception of former events.

Metacontrast masking is a special form of backward masking in which the mask does not spatially overlap with the target (Breitmeyer & Ögmen, 2006). The reduction of the target's visibility, the so-called masking effect, is influenced by the temporal gap between the target and mask onset, the so-called stimulus-onset asynchrony (SOA; figure 1a). On average, the masking effect is equally weak in short and long SOA and strongest for medium SOA in which the target is often reported to be not visible at all. This U-shaped course of the masking effect as a function of the SOA is called the masking function. Core questions that theories on metacontrast masking should be able to explain are (1) how the mask is able to reduce the visibility of the target despite the target is presented first and (2) why the maximum reduction of the target's visibility occurs in medium SOA. Finding answers to these questions is not only important for understanding the masking phenomenon but would also provide insights into other fields of research that apply the metacontrast masking paradigm, e.g. the investigation of the mechanisms of visual perception (Breitmeyer & Ögmen, 2006; Bachmann & Hudetz, 2014), the mechanisms of unconscious information processing (e.g. Neumann & Klotz, 1994; Vorberg et al., 2003; Mattler, 2003, 2005, 2006), the neural correlates of visual awareness (Railo & Koivisto, 2009; Del Cul et al., 2007; van Aalderen-Smeets et al., 2006), clinical anomalies like schizophrenia (Green et al., 1997) and intelligence (Nettelbeck, 2001).

One of the most influential theories on metacontrast masking is the dual-channel sustained-transient approach (Kulikowski & Tolhurst, 1973; Tolhurst, 1973) and its updated version the neural model of retino-cortical dynamics (RECOD; Ögmen, 1993; Breitmeyer & Ögmen, 2000). According to these theories, stimulus processing takes place in two different channels that differ from each other in processing speed. While coarse patterns and the spatial location of a stimulus are processed in a fast transient channel, stimulus features are processed in a slow sustained channel. Metacontrast masking is proposed to result from an inter-channel inhibition in which the fast transient channel activity of the mask inhibits the slow sustained channel activity of the target. This would explain the maximum masking effect for medium SOA since only the transient activity of a delayed mask would show a perfect temporal overlap with the sustained activity of the target. Although the theory is able to explain the findings of many studies on visual masking, it is unclear whether the mechanisms that the theory proposes work as described (Francis, 1997).

An alternative approach to explain the masking phenomenon is provided by the boundary contour and feature contour system (Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994). Core to this approach is the assumption that a stimulus' contour and surface are processed in different pathways and that the completion of the contour processing is a prerequisite for the surface processing to start (Breitmeyer & Jacob, 2012). After the offset of a stimulus, its contour signals slowly start to erode which under normal circumstances would not be fast enough to impair its surface processing. Metacontrast masking is described to result from lateral inhibition in which cells that process the contours of the mask inhibit the cells that process the contours of the target (Francis, 1997). This effect would be strongest in medium SOA since the erosion of the target's contour signals would have already started and be most susceptible to the lateral inhibition of the mask. The erosion of the target's contour signals before the processing of its surface finishes would lead to a reduced visibility of the target and hence masking.

In both of the presented masking theories, masking is explained to result from disrupting target processing due to the inhibitory influence of the mask. Accordingly, it was proposed that the stronger target processing is, the less prone it is to the inhibitory influence of the mask (Francis, 1997). This is supported by evidence on the neural correlates of masking that resulted from contrasting trials with a masked and unmasked perception of the target-mask sequence while keeping physical presentation parameters constant. Against this background, masking of the target has been demonstrated to occur more likely when the target is presented in the trough of the neural alpha oscillation (Mathewson et al., 2009). This phase effect interacted with the power and only occurred when the alpha power was high. The authors propose that the alpha oscillation reflects a periodic variation of the neural excitability that affects stimulus processing. The trough of the alpha cycle and hence its most negative phase interval would correspond to a maximum inhibition of the underlying neural substrate and reduce the quality of all stimuli that are processed in this time interval. Consequently, the target would be more susceptible to the inhibitory influence of the mask if its neural processing coincides with the trough of the alpha cycle.

One further neural correlate of masking that might indicate the protective effect of a strong target processing against the inhibitory influence of the mask is the visual awareness negativity (VAN; Railo et al., 2011; Förster et al., 2020). This neural correlate is not restricted to metacontrast masking but has been associated with visual awareness in general. In metacontrast masking, the VAN reflects a greater negativity mostly in the N1-N2 time range for trials with an unmasked compared to a masked perception. Its occipito-temporal topography suggests that the VAN reflects a process in the ventral stream. Since TMS on early visual areas shortly after target presentation reduces the visibility of the target (Railo & Koivisto, 2012), the VAN may reflect target specific reverberating feedforward activity (Railo et al., 2011). Accordingly, the VAN would indicate a strong target processing that is less prone to the inhibitory influence of the mask. Although a more positive P1 and P3 have also been repeatedly been associated with an unmasked perception, they likely reflect sensory and post-perceptual processes rather than processes associated with visual awareness and masking itself (Railo et al., 2011; Förster et al., 2020).

All of the presented neural correlates of masking are based on the comparison of masked and unmasked trials and the assumption that these trials only differ from each other with respect to the visibility of the target. Most masking theories would share this assumption that the masking function reflects a single unidimensional mechanism that affects target visibility. Lately, this assumption has been questioned by findings demonstrating that the perceptual quality of the target-mask sequence differs between short and long SOA (Reeves, 1982; Francis & Cho, 2008; Jannati & Di Lollo, 2012; Sackur, 2013) and factor analytical results that imply at least three mechanisms to partake in the generation of the masking function (Albrecht & Mattler, 2016). Even without any prior training, participants were demonstrated to report around seven different perceptual qualities in a metacontrast masking paradigm (Koster et al., 2020). Importantly, the proportions of each reported perceptual quality were correlated to the objective task performance demonstrating the validity and significance of participants' perceptual reports. In sum, the masking function is likely the result of not one but multiple mechanisms.

1.3 Bridge building between temporal and masking research

Temporal mechanisms are mentioned throughout the metacontrast masking literature to partake in metacontrast masking (Werner, 1935; Reeves, 1982; Francis & Cho, 2008; Jannati & Di Lollo, 2012; Sackur, 2013; Albrecht & Mattler, 2016; Koster et al., 2020). This is especially evident since participants regularly report to perceive the target inside of the mask despite both stimuli are never simultaneously presented on screen (see e.g. Koster et al., 2020). Accordingly, temporal integration has been discussed to either induce masking or save the target from masking (Francis & Cho, 2008). In his dual-process theory of metacontrast masking, Reeves (1982) even postulates that the masking function results from two independent temporal mechanisms alone without assuming any masking mechanism. He postulates a competition between a temporal integration mechanism that fuses the target-mask sequence into a single percept and a temporal segregation mechanism that places target and mask into different percepts. While the strength of the temporal integration mechanism is maximal in short SOA and continuously declines with increasing SOA, the strength of the temporal segregation mechanism is maximal in long SOA and continuously declines with decreasing SOA. In medium SOA, both mechanisms are equally strong and hence the likelihood for both of them to fail at the same time maximal. According to Reeves (1982), a concurrent failure of both temporal integration and segregation mechanisms results in masking which would hence reflect the absence of any successful temporal processing of the target-mask sequence (figure 3). To test his theory, Reeves conducted a metacontrast masking experiment and asked his participants to first report on the visibility of the target and then the temporal succession of the target-mask sequence. His findings support his theory by demonstrating that a temporally integrated percept of the target-mask sequence is maximal in short SOA and continuously declines with increasing SOA while a temporally segregated percept showed the reversed pattern. In addition, the rated visibility of the target showed a U-shaped course as a function of the SOA; Masking was hence maximal in medium SOA.

Despite the proposed relevance of temporal mechanisms in metacontrast masking, temporal and masking mechanisms have only rarely been concurrently

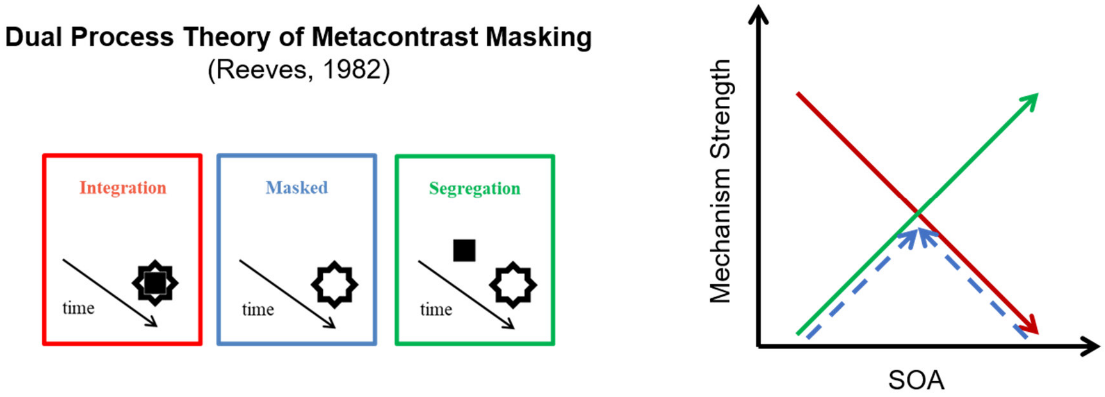

Figure 3. Illustration of the dual process theory of metacontrast masking (Reeves, 1982). According to this theory, there are three possible perceptual impressions of the target-mask sequence: (1) a temporally integrated, (2) a temporally segregated and (3) a masked perception. Masked perceptions are proposed to result from a concurrent failure of a temporal integration and segregation mechanisms. These temporal mechanisms are proposed to be independent and their strengths are proposed to show a reversed course as a function of the SOA. Since temporal integration and segregation mechanism are equally strong in medium SOA, the probability of both of them failing at the same time is maximal here. Accordingly, masking should be maximal in medium SOA.

investigated. This is especially curious since both fields of research share many similarities. On a methodological level, their paradigms are based on the presentation of two successive short-lived stimuli. On an empirical level, their neural correlates consist of pre-stimulus phase differences especially in the alpha frequency band as well as ERP differences in the N2 and P3 time windows. On a theoretical level, periodic variations of the neural excitability due to neural oscillations have been hypothesized to explain both temporal and masking effects.

Though these similarities may be purely by chance, they may also indicate that both fields of research investigate at least partially the same underlying mechanisms of our visual perception despite labelling them differently. This idea would be in line with Reeves' (1982) proposition that masking is the product of a concurrent failure of both temporal integration and segregation mechanisms. A concurrent investigation of temporal and masking mechanisms would allow us to test Reeves' (1982) proposition and further illuminate the relationship between temporal and masking phenomena.

Although it may sound like that solely masking research would profit from considering temporal mechanisms, temporal research would profit to a similar degree from considering masking mechanisms. In this field of research, the neural correlates of temporal integration and segregation were investigated by comparing trials with a successful to a failed temporal integration (and segregation). Most likely due to the assumption of a temporal antagonism in which a failed temporal integration automatically results in a successful temporal segregation, this comparison was only rarely questioned to reflect something different than a differential temporal processing of the stimulus presentation. In the missing element task for example, it is undisputed that a successful identification of the missing element results from a successful temporal integration. A failed identification of the missing element, however, may result from various mechanisms of which a successful temporal segregation is only one. Another mechanism would be masking which reduces the visibility of either the first (backward masking) or second grid (forward masking) due to the presentation of the other grid. Eventually, perceiving only one of the grids due to masking is not sufficient to identify the missing element. Therefore, a comparison of trials with a successful and a failed temporal integration in the missing element task may not only reflect temporal but also other mechanisms like masking. A potential masking confound in temporal research has never before been investigated but pointed out (Wutz et al., 2014; Akyürek & Wijnja, 2019) and also generalizes to other temporal paradigms like the two-flash task. Accordingly, temporal research would also profit from a concurrent investigation of temporal and masking mechanisms.

The following studies were intended to build a bridge between the research fields on temporal and masking mechanisms. In each study, we used a metacontrast masking paradigm and asked our participants to report on each trial on their phenomenal perception of the target-mask sequence while their neural signals were continuously recorded. Participants could either report (1) a temporally integrated percept when they perceived the target inside of the mask, (2) a temporally segregated percept when they perceived the target-mask sequence as a succession or (3) a masked perception in which the mask but not the target was visible. We decided to use a phenomenological compared to a performance-based approach in all of our studies since it allowed us to measure the perceptual content of our participants which may quickly change from trial to trial. Though phenomenological approaches have been criticized to be affected by response biases that may render their findings inconclusive (Nisbett, 1977; Vermersch, 1999; Velmans, 2007), they have been used previously in metacontrast masking paradigms and were demonstrated to be correlated to performance-based measures (Reeves, 1982; Koster et al., 2020). Accordingly, we view phenomenological approaches as a complementary methodology that provides information that would be otherwise inaccessible through performance-based approaches.

Eventually, we compared the neural signals between the different phenomenal perceptions to identify the neural correlates of temporal and masking mechanisms. These findings helped us answer our main questions (1) whether temporal processes are relevant in metacontrast masking, (2) how temporal and masking processes are related to each other and (3) whether established paradigms to investigate temporal mechanisms are confounded by a masking mechanism.

2. Empirical investigations

In the following, the results of three studies will be presented. While study one and two were designed to exclusively investigate the neural correlates of temporal mechanisms in the metacontrast masking paradigm, study three was designed to concurrently investigate the neural correlates of both temporal and masking mechanisms in the metacontrast masking paradigm and to compare them to the neural correlates of temporal mechanisms that can be found in well-established temporal paradigms. While each study will only be summarized here, the full manuscript to each study can be found in the appendix.

2.1 First study:

Neural correlates of temporal integration and segregation in metacontrast masking: a phenomenological study

Although temporal mechanisms have been proposed to play a crucial role in metacontrast masking and the generation of the masking function, their neural correlates have never before been investigated in a metacontrast masking paradigm. Accordingly, this study is the first to investigate the neural correlates of temporal mechanisms in a metacontrast masking paradigm. To do so, we asked our participants on each trial to report whether they perceived the target-mask sequence as either temporally integrated, temporally segregated or masked. For each participant, we determined in a first session one SOA for which temporally integrated and segregated percepts were reported with equal proportions and presented this SOA in half of all trials in the second session in which we also continuously recorded our participants' neural signals with an EEG. In this way, we got as many trials for both temporally integrated and segregated reports as possible while keeping physical presentation parameters constant. Only these trials were forwarded to the neural data analysis in which temporally integrated and segregated reports were compared to each other.

With regard to our behavioral data, we found the report proportions of a temporally integrated percept to be maximal at short SOA and to decrease with increasing SOA while the opposite pattern was shown by the report proportions of temporally segregated percepts. In addition, report proportions of masked percepts showed a reverse U-shaped course as a function of the SOA and were maximal in medium SOA. These findings replicate previous behavioral findings in the metacontrast masking paradigm that used a phenomenological approach (Reeves, 1982; Koster et al., 2022) and are in line with Reeves' (1982) dual process theory of metacontrast masking.

With regard to our neural data, we found pre-stimulus phase differences in the alpha and beta frequency band. Although phase differences in the beta frequency band have not been demonstrated in the visual domain before, phase differences in the alpha frequency band have repeatedly been associated with temporal processing (see e.g. VanRullen, 2016a). In addition, we found post-stimulus ERP differences that indicated a more negative ERP between 200 and 450 ms for trials with a temporally integrated percept. A similar effect was demonstrated for the missing element task and was interpreted as a larger engagement of spatial integration mechanisms that a successful temporal integration of the stimulus sequence incurs (Akyürek et al., 2010).

Taken together, our findings indicate that the same neural correlates of temporal mechanisms that have been demonstrated for established temporal paradigms can also be found in a metacontrast masking paradigm. This also validates our phenomenological approach since established temporal paradigms are mostly based on performance-based approaches.

2.2 Second study:

Neural sources of temporal integration and segregation in metacontrast masking: a MEG study

Although our first study was a successful first step towards a concurrent investigation of temporal and masking mechanisms, our conclusions were based on the neural data of only 15 participants. In addition, we demonstrated pre-stimulus phase differences in the beta frequency band to be associated with temporal processing which has only been demonstrated for the auditory (Fujioka et al., 2012; Arnal et al., 2015) and somatosensory (Baumgarten et al., 2015) domain before but not for the visual domain. Thus, to ensure the reliability of our previous results, one aim of our second study was to replicate them.

In contrast to our first study, in which we recorded the neural signals with an EEG, we used a MEG for our second study which provided us with an optimal setup to localize neural signals in source space. Neural correlates of temporal mechanisms have only seldomly been projected into source space or investigated with devices that provide a good spatial resolution (see e.g. Wutz et al., 2016). In comparison, fMRI studies have associated an occipito-temporal dialogue to be essential for the masking effect (Haynes et al., 2005; Imamoglu et al., 2014). In addition, parietal, frontal and subcortical brain areas were also implied to be involved in the generation of the masking effect (Haynes et al., 2005;

Imamoglu et al., 2014; Albrecht et al., 2013). Since Reeves' (1982) dual-process theory of metacontrast masking hypothesizes that masking results in the absence of temporal processing, temporal mechanisms should account for the masking phenomenon. Accordingly, the neural sources of temporal and masking mechanisms should be very similar if not identical to each other. To examine this hypothesis, we determined the neural sources of temporal integration and segregation and compared them to those reported for the masking phenomenon.

To do so, we once again asked our participants to report on each trial of a metacontrast masking paradigm whether they perceived the target-mask sequence temporally integrated, temporally segregated or masked. While participants trained the task in a first session, their neural signals were only recorded in a second session. In the beginning of the second session, we determined for each participant one SOA for which temporal integration and temporal segregation were reported to the same degree and presented this SOA in half of all trials for the remainder of the experiment. In this way, we got as many trials for both temporally integrated and segregated reports as possible while keeping physical presentation parameters constant. Only these trials were forwarded to the neural data analysis in which temporally integrated and segregated reports were compared to each other in source space.

Our results demonstrated pre-stimulus phase differences in the theta, alpha and beta frequency band. On the one hand, theta and alpha phase differences were localized in occipito-temporal brain areas which may indicate that lower frequency bands are associated with bottom-up temporal processing. These neural sources would fit previous findings that travelling waves in the alpha frequency band explain temporal effects in the missing element task (Vanbecelaere et al.,

2019) and the idea that neural representations are generated in the ventral stream (Goodale & Milner, 1992; Milner & Goodale, 2008). On the other hand, beta phase differences were localized in fronto-temporal brain areas which may indicate their involvement in a top-down influence of frontal brain areas that biases neural processing further down in the neural hierarchy (see e.g. Buschman & Miller, 2007; Castellano et al., 2014). In addition, we found ERF differences inter alia 385 ms after target presentation indicating a greater neural activation for temporal integration.

Both our pre-stimulus phase differences and post-stimulus ERF differences replicated our previous findings in our first study. This ensured the reliability of our previous results and indicated once again that the neural correlates of temporal integration and segregation can also be demonstrated in a metacontrast masking paradigm. In addition, sources of temporal and masking mechanism show a considerable overlap. Occipito-temporal brain areas as well as frontal brain areas have not only been implicated in our findings but also in masking studies (Haynes et al., 2005; Albrecht et al., 2013; Imamoglu et al., 2014). However, although similar brain areas are implicated in both temporal and masking phenomena they may not reflect the same underlying mechanisms. This is especially the case since our neural sources of temporal mechanisms were mainly based on phase effects while neural sources of masking effects were based on fMRI results.

2.3 Study 3:

Neural correlates of temporal and masking mechanisms: a concurrent investigation in a multi-paradigm study

Although our previous results supported the notion that temporal mechanisms are active in the metacontrast masking paradigm, the relationship between temporal and masking mechanisms remained speculative. Our third study was designed to get a better understanding of this relationship by concurrently investigating the neural correlates of temporal and masking mechanisms. To do so, we conducted a metacontrast masking experiment and asked participant once again to report on each trial whether they perceived the target-mask sequence temporally integrated, temporally segregated or masked. Just like in our previous studies, our aim was to find for each participant one physical presentation condition for which each percept is reported equally often. However, our previous behavioral data suggested that the SOA with an optimal ratio between report proportions of the temporal percepts and an optimal report proportion of the masking percept seldomly coincide on an individual level. Based on an extensive amount of piloting we decided to adjust the ratio between report proportions of the temporal percepts by varying the SOA and to adjust the masking proportion by additionally varying the mask size while keeping the target-mask distance constant.

Overall, the metacontrast masking experiment consisted of two training sessions and two recording sessions in which we continuously recorded the neural signals of our participants with an EEG. While we dedicated the first session purely to the training of the task, we determined in the second session for each participant one SOA and mask size for which each percept was reported equally often. This set of parameters was then presented in half of all trials in the third and fourth (recording) session and was adjusted if necessary after each block to guarantee that each percept was reported often enough. By only extracting these trials for the final neural analyses we got as many trials for each percept report as possible while still keeping physical presentation parameters (statistically) constant. Eventually, we compared the ERP between each percept.

Our results demonstrated the visual awareness negativity and late positivity for the comparison of both the temporally integrated and temporally segregated percept against the masked percept. These neural correlates of masking have previously been only investigated in the metacontrast masking paradigm with performance-based approaches (Railo et al., 2011; Förster et al., 2020). Our replication of these effects therefore further validates our phenomenological approach. In addition, we found a more negative ERP for centro-parietal electrodes between 200 and 450 ms for both the temporally integrated and masked percept when compared against the temporally segregated percept. These findings replicate our previous findings that we interpreted as a greater engagement of spatial integration mechanisms for the temporally integrated percept (Akyürek et al., 2010). Since the masked percept depicted the same result, a spatio-temporal integration mechanism may also be crucial for masking to occur.

To evaluate the degree of shared processes between paradigms that investigate temporal mechanisms, we additionally conducted the missing element and two-flash task with the same participants in three further sessions. While the fifth session was dedicated to the training of both tasks, the sixth and seventh session were each dedicated to one task specifically in which also the neural signals of our participants were recorded with an EEG. For both tasks, we determined in the fifth session one ISI for which correct and incorrect reports showed equal proportions and presented this ISI in half of all trials in the sixth and seventh session. This ISI was adjusted if necessary after each block to ensure a sufficient amount of trials for both correct and incorrect reports under otherwise constant physical presentation conditions. Only these trials were then forwarded to the final neural data analyses in which the ERP between correct and incorrect reports were compared against each other.

Our findings indicated a more positive P1 for incorrect reports in the two-flash task which fits nicely to previous results demonstrating that a more positive P1 corresponds to an increased attentional deployment (Hillyard & Anllo-Vento, 1998) which in turn has been associated with a decreased temporal resolution (Yeshurun & Levy, 2003). Thus, the more participants attended to the location of the two-flash presentation, the less likely they are to correctly perceive them as a succession of two events. In addition, we found a more positive late P3 for correct reports in the missing element task which replicates previous findings that interpreted this effect as a decreased neural effort to consolidate one compared to two events in memory (Akyürek et al., 2010). The only shared ERP difference between paradigms was a more negative N1 for correct reports in the missing element task which was also demonstrated for the temporally integrated percept when compared against the masked percept in the metacontrast masking task. This shared finding may indicate a potential masking confound in the missing element task and would fit our additional finding that the behavioral data of the missing element and metacontrast masking task are related to each other. However, the N1 effect in both paradigms was only marginally significant and should hence be interpreted with caution.

Overall, our results replicated not only our previous temporal effects but also the neural correlates of masking and extend them by the implication that a spatio-temporal integration mechanism may be relevant for masking. This finding fits well into the framework of the boundary contour and feature contour systems

(Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994; Francis, 1997; Breitmeyer & Jacob, 2012) and might indicate that the inhibitory influence of the mask is increased (or enabled) when the target-mask sequence is spatio-temporally integrated with the mask. This potential dependence of temporal integration and masking mechanisms, however, is hardly to be aligned with Reeves (1982) dual process theory of metacontrast and the assumption that masking results in the absence of temporal processing. In addition, we found indications of a shared mechanism in the metacontrast masking and missing element task which may indicate a potential masking confound of established temporal paradigms. An outline of preliminary findings on the power and phase data to this study can be found in the supplements to this manuscript (*Appendix II - manuscript for study 2*).

3. General discussion

Research on temporal and masking mechanisms share both theoretical, methodological and empirical similarities creating the impression that they might investigate the same underlying aspect of our neural system. However, there is hardly any overlap between these fields of research. Thus, the general aim of my PhD was to build a bridge between the temporal and masking research and to investigate the relationship between temporal and masking mechanisms. To do so, we performed in each of our studies metacontrast masking experiments in which we asked participants to report on each trial whether they perceived the target-mask sequence temporally integrated, temporally segregated or masked while their neural signals were continuously recorded. Eventually, we compared the neural signals between percept reports and applied both time-frequency and ERP analyses.

As a first step towards the unification of both fields of research, we demonstrated in our first and second study that the neural correlates of temporal mechanisms can be found in the metacontrast masking paradigm. Specifically, we found both pre-stimulus phase differences in the theta, alpha and beta frequency band and post-stimulus ERP differences that have repeatedly been associated with temporal mechanisms. On this basis, our third study was designed to concurrently investigate the neural correlates of temporal and masking mechanisms in a metacontrast masking paradigm. In the very same study, we additionally conducted a missing element and two-flash task to evaluate the degree of shared mechanisms between paradigms that investigate temporal mechanisms. With respect to the metacontrast masking task, our results not only replicated our previous results but also implicated the relevance of a spatio-temporal integration mechanism in the masking phenomenon. In addition, we found indications of a shared mechanism in the metacontrast masking and missing element task which might constitute a masking mechanism.

3.1 Temporal mechanisms in masking paradigms

The behavioral data of each of our metacontrast masking experiments demonstrated the same pattern of results in which the proportion of temporally integrated reports were maximal in short SOA and decreased with increasing SOA while the proportion of temporally segregated reports showed the reversed course. These findings replicate former studies that used a phenomenological approach and asked participants, inter alia, to evaluate their temporal perception of the target-mask sequence (Reeves, 1982; Koster et al., 2020). In addition, they are in line with the dual process theory of metacontrast (Reeves, 1982) that proposes two independent temporal mechanisms of which the temporal integration is strongest in short SOA and becomes weaker with increasing SOA while the temporal segregation shows the reversed course. According to this theory, masking results in the absence of any temporal processing and should hence be maximal in medium SOA since both temporal mechanisms are equally strong there. This is in line with our findings that show a maximum proportion of masked reports in medium SOA.

3.1.1 Pre-stimulus phase differences

By comparing the neural signals between temporally integrated and segregated reports of the target-mask sequence, we could demonstrate, inter alia, pre-stimulus alpha and theta phase differences. Pre-stimulus phase differences in lower frequency bands have repeatedly been associated with temporal processing (Varela et al., 1981; Samaha & Postle, 2015; Milton & Pleydell-Pearce, 2016; VanRullen, 2016a; Wutz et al., 2016; Ronconi & Melcher, 2017; Ronconi et al., 2017; Battaglini et al., 2020; Herzog et al., 2020) and been postulated to reflect a periodic variation of the neural excitability that produce time windows of better and worse neural processing (Hanslmayr et al., 2013; Jensen et al., 2014). Accordingly, our pre-stimulus phase differences emphasize the relevance of temporal mechanisms in metacontrast masking and support approaches that postulate a generation of the masking function through multiple, inter alia temporal, mechanisms (Reeves, 1982; Francis & Cho, 2008; Jannati & Di Lollo, 2012; Sackur, 2013; Albrecht & Mattler, 2016; Koster et al., 2020).

We localized the sources of this alpha and theta phase effect in occipito-temporal brain areas which is in line with the model of two visual systems according to which sensory representations are formed in the ventral stream (Goodale & Milner, 1992; Milner & Goodale, 2008). Although each of the implicated brain areas might produce their own alpha and theta oscillations, it might also be possible that a travelling wave of alpha and theta activity propagates from occipital to temporal brain areas. Travelling waves of neural activity have been demonstrated for the alpha oscillation (Fellinger et al., 2012; Lozano-Soldevilla & VanRullen, 2019) and were demonstrated to explain temporal effects in the missing element task (Vanbecelaere et al., 2019). The advantage of a travelling wave in temporal processing would be that the same time code is kept throughout each processing step in the neural hierarchy. Overall, our theta and alpha phase effects might reflect a bottom-up temporal mechanism.

While alpha phase differences have been found in occipital electrodes and have been related to a sensory sampling rhythm, theta phase differences have been found in fronto-central electrodes and have been related to an attentional sampling rhythm (VanRullen, 2016a). Though these findings are in line with our alpha phase effects, they are in conflict with our theta phase effects that showed the same source localization as our alpha phase effects. An allocation of neural frequencies exclusively to specific brain areas may hence be too simplified. A pre-stimulus occipito-temporal phase effect for both the alpha and theta frequency band has been demonstrated before in a two-flash task (Ronconi et al., 2017). However, the authors did not find both effects concurrently. While an optimization of the flash presentation for a fused percept (ISI = 40 ms) resulted in an alpha phase effect, an optimization for an apparent motion percept (ISI = 120 ms) resulted in a theta phase effect. Both perceptual impressions have also been reported for the metacontrast masking paradigm (Albrecht & Mattler, 2012; Koster et al., 2020). Accordingly, our target-mask stimulation may have engaged multiple oscillatory rhythms whose differential temporal processing may have resulted in more complex percepts than initially assumed.

Curiously, although it is postulated that phase effects reflect variations in neural excitability around stimulus presentation that influence their temporal processing, our phase effects and those reported in the literature are restricted to the pre-stimulus time window. Brüers and VanRullen (2017) explained this discrepancy by demonstrating that target-evoked ERP and signal filtering (that is commonly used in time-frequency analyses) contaminate the oscillatory signal and render any phase effect around the stimulus presentation insignificant. However, due to the stability of an oscillatory cycle, phase effects can still be detected in the pre-stimulus time window and hence outside of the time window of post-stimulus contamination. By eliminating the influence of post-stimulus neural activity on the oscillatory signal, the authors demonstrate that phase effects would actually be most pronounced shortly after stimulus presentation.

Beta phase effects on temporal processing have been limited to the auditory (Fujioka et al., 2012; Arnal et al., 2015) and somatosensory domain (Baumgarten et al., 2015) and have never before been demonstrated for the visual domain. However, we repeatedly demonstrated a pre-stimulus beta phase effect on the temporal processing of the target-mask sequence. This finding is especially curious since the amplitude of the neural beta frequency is smaller than that of the theta and alpha frequency and hence has a smaller potential to periodically variate the neural excitability to influence temporal processing. Our results may hence demonstrate that the amplitude of the beta frequency band is still large enough to create time windows of better and worse neural processing.

However, the general interpretation of phase effects to reflect periodic variations in neural excitability has been questioned (Milton & Pleydell-Pearce, 2016). Such a hypothesis would predict that phase effects should interact with the power and exert a larger influence on temporal processing when the power is high. Since the authors could not find such an interaction, they suggested that pre-stimulus phase effects are independent from power effects and reflect differences in fundamental periodicities in our neural communication. Combining this idea with the results of our source analysis, our beta phase effects might also reflect a fundamental periodicity between frontal and temporal brain areas. Specifically, we could demonstrate in our second study that beta phase effects were first localized in the left dorsolateral prefrontal cortex and then spread into temporal brain areas of the right hemisphere.

Frontal brain areas have been associated with a variety of high-level brain functions (MacDonald et al., 2000; Heekeren et al., 2006) that might exert their influence through biasing brain areas further down in the hierarchy (Desimone & Duncan, 1995; Miller, 2000; Braver et al., 2002). In line with this reasoning, beta phase coherences between frontal and parietal brain areas have already been associated with contour integration mechanisms (Castellano et al., 2014) and the deployment of attention (Buschman & Miller, 2007). In addition, beta oscillations in general have been associated with a top-down influence on cognitive mechanisms by maintaining the current cognitive state (Engel & Fries, 2010). Accordingly, beta oscillations may represent the neural transmitter frequency through which frontal brain areas bias local competitive activations further down in the neural hierarchy. Thus, our beta phase effects may reflect a top-down mechanism through which the temporal processing and perception of the target-mask sequence is influenced.

3.1.2 Post-stimulus ERP differences

In each of our metacontrast masking experiments, we found a more negative ERP around 200 to 450 ms for temporally integrated compared to temporally segregated percepts that has also been demonstrated for the missing element task before (Akyürek et al., 2010). The authors of this study interpreted this result to reflect a spatial integration mechanism that is more engaged for a temporally integrated than a temporally segregated percept. This finding is similar to the contour integration negativity (CIN) that has been demonstrated by comparing sets of line segments whose orientations were either arranged randomly or in such a way that contours were perceivable (Pitts & Martinez, 2014). By comparing these conditions, the set of line segments with perceivable contours showed a more negative ERP amplitude between 150 and 300 ms in parieto-occipital electrodes. This likely indicates a spatial integration mechanism that is more engaged the more contours it needs to simultaneously process.

Differences in the integration of contours may also explain our results. On the one hand, a temporal integration of the target-mask sequence may have engaged contour mechanisms for each stimulus at the same time leading to a more condensed accumulation of the associated neural activity. On the other hand, a simultaneous perception of both the target and mask contours results in a small gap in between both stimuli and hence an additional contour. In both cases, our ERP effect may reflect the CIN and hence a more engaged contour integration mechanism for temporally integrated percepts. In contrast to the original effect, in which single stimulus displays with varying contour information were compared against each other, our paradigm consisted of the presentation of two stimuli and differences in contour information could only arise as soon as the processing of each the target and mask stimulus was finished and their potential spatio-temporal integration took place. This reasoning would explain why we find the CIN in later time windows and in more frontal electrodes compared to the original effect. It remains up to discussion whether the CIN in our study reflects a consequence of a previously successful temporal integration or marks the time point at which both temporal and spatial processes come into effect.

3.2 Relating temporal and masking mechanisms

The source localization of our phase effects implied both occipito-temporal as well as fronto-temporal areas to participate in the temporal processing of the target-mask sequence. These brain areas have also been implied for the masking phenomenon (Haynes et al., 2005; Imamoglu et al., 2014). However, our source data cannot establish a definite link between temporal and masking mechanisms since a participation of the same brain areas in both mechanisms does not automatically imply a common mechanism behind both of them. Similarly, although our behavioral data are in accordance with the dual process theory of metacontrast masking (Reeves, 1982), they do not confirm its underlying mechanisms. Accordingly, to identify shared neural effects that in turn would indicate a shared mechanism, we concurrently investigated the neural correlates of temporal and masking mechanisms in our third study.

We demonstrated a more negative ERP in the N1-N2 time range and occipito-temporal electrodes and a more positive ERP in the late P3 time window in centro-parietal electrodes for both temporally integrated and segregated reports when compared against masked reports. These ERP differences likely reflect the VAN and late positivity that have previously been associated with the comparison of masked and unmasked reports (Railo et al., 2011; Förster et al., 2020). While the late positivity has been associated with post-perceptual processes in working memory (van Aalderen-Smeets et al., 2006), the VAN is handled as a candidate for the neural correlate of consciousness. In addition, we found a more negative ERP between 200 and 450 ms in centro-parietal electrodes for masked reports when compared against temporally segregated reports. This is the same effect that we have also found for temporally integrated reports when compared against temporally segregated reports and that we have associated with the CIN (Pitts & Martinez, 2014). Since a spatial integration without a prior temporal integration of the two successively presented stimuli seems unlikely, I want to conclude that the same spatio-temporal integration mechanism that results in a temporally integrated perception of the target-mask sequence may also partake in their masked perception.

Though a masked perception in which nothing of the target and only the mask is perceivable seems not to be related to a spatio-temporal integration mechanism at first sight, they can be well aligned in the framework of the boundary contour and feature contour systems (Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994). In this framework, target processing takes place in two different systems: a system that processes its contour and a system that processes its surface. Since the surface system is dependent on the contour signal, surface processing takes place after the processing of the contour is finished (Breitmeyer & Jacob, 2012). Thus, factors that compromise the contour signal also compromise surface processing. One factor that is inherent to the contour processing system is an erosion of the contour signal after the offset of the target. Under normal circumstances in which the target is presented long enough and in the absence of any other stimulus, this erosion is slow enough and does not compromise surface processing. Accordingly, the target would be clearly visible. However, the erosion can be sped up, for example through cells that process the contour of the mask and exercise a lateral inhibition on the neighboring cells that process the contour of the target. The maximum effect of such a lateral inhibition would be exerted in medium SOA since the erosion of the target's contours would have already started. Accordingly, the target's contour signal could reach critical levels of erosion before its surface processing is finished. In this case, the target's visibility would be impaired and masking would result.

According to Francis (1997), two factors compete against each other in this framework to determine the degree of masking: (1) the strength of the excitatory feedback activity of the target's contour signal and (2) the strength of the lateral inhibition. These factors could be associated with our ERP differences. The strength of the excitatory feedback activity of the target's contour signal could be reflected by the VAN since it was associated with a target-related reverberating feedforward activity within the ventral stream (Railo et al., 2011). In addition, a spatio-temporal integration of the target and mask, reflected by the CIN, may enhance the mask's lateral inhibition of the target's contour. One way to think about this effect is that masking benefits from the concurrent processing of the target-mask sequence in the same temporal integration window. The resulting spatio-temporal proximity between cells that process both the target and mask stimulus may enhance the mask's lateral inhibition to affect the processing of the target's contours. Overall, temporally integrated and masked percepts would share the same spatio-temporal integration mechanism (reflected by the CIN) but differ in the strength of their target-related excitatory feedback activity (reflected by the VAN).

Though our results can be explained in the framework of the boundary contour and feature contour systems they are much harder to be aligned with Reeves' (1982) dual process theory of metacontrast masking. In this theory, masking should result from the concurrent failure of both a temporal integration and segregation of the target-mask sequence. Therefore, a masked percept should not share any neural correlates of temporal integration or segregation mechanisms. However, we found a CIN for both the temporally integrated and masked percepts when compared to the temporally segregated percept. Assuming that the CIN indicates a spatio-temporal integration of the target-mask sequence, our findings would indicate that masking benefits from a spatio-temporal integration of the target-mask sequence which would run counter to the implications of the dual process theory of metacontrast masking. However, there is one study whose findings imply that a spatial integration of two successively presented stimuli can occur even in the absence of their temporal integration (Drewes et al., 2014). Accordingly, the CIN might only reflect a shared spatial integration mechanism for the temporally integrated and masked percept. In principle, this would still be compatible with the dual process theory of metacontrast masking since no shared temporal mechanism would be implied. To empirically investigate whether a temporal integration can be associated with both temporally integrated and masked percepts, their pre-stimulus phase data should not show any difference and hence indicate a comparable temporal processing of the target-mask sequence. Though not right now, our analyses will eventually provide the results to evaluate this prediction.

3.3 Masking mechanisms in temporal paradigms

The occurrence of masking mechanisms in temporal paradigms has been proposed (Wutz et al., 2014; Akyürek & Wijnja, 2019) but never been systematically investigated. Incorrect reports in the missing element task may result from a failed temporal integration but may also be due to one grid masking the other. Similarly, an incorrect report in the two-flash task may result from a failed temporal segregation but may also be due to one flash masking the other. In both paradigms neural effects are usually determined by comparing correct and incorrect reports which may thus reflect both temporal as well as masking mechanisms. Separating temporal from masking effects is especially important since their neural correlates are quite similar to each other. Both temporal (Varela et al., 1981; Milton & Pleydell-Pearce, 2016; VanRullen, 2016a; Ronconi et al., 2017) and masking effects (Mathewson et al., 2009) have, for example, been associated with pre-stimulus alpha phase differences and were hence both proposed to result from periodic variations in the neural excitability due to neural oscillations.

The behavioral data of our third study indicated a shared mechanism for both the metacontrast masking and the missing element task. Specifically, we determined for each task and participant the point of subjective equality (PSE) for which equal proportions of temporally integrated (correct) and temporally segregated (incorrect) reports were made. These PSE showed a significant positive correlation. One way to interpret this result is to propose a shared temporal mechanism whose individual variance affects both tasks in the same way. Samaha and Postle (2015) for example demonstrated in a two-flash task that the individual alpha frequency was correlated to the temporal resolution of our visual system and hence the size of temporal integration windows. Accordingly, it may be the case that the same individually variable neural oscillation affects the temporal processing of both the metacontrast masking and missing element task. However, it is unlikely that this neural oscillation reflects the individual alpha frequency since we (1) demonstrated no relationship between the PSE and the individual alpha frequency in our first study (see the supplements in *Appendix I - manuscript for study 1*) and (2) found no relationship between the PSE of either the metacontrast masking nor the missing element task with the PSE of the two-flash task for which such a relationship was demonstrated.

Alternatively, the shared mechanism between the metacontrast masking and missing element task may constitute a masking mechanism. This is indicated by a shared N1 effect for both tasks. For the missing element task, correct compared to incorrect reports showed a more negative N1. Since incorrect reports may also result from masking, this effect may reflect a more negative N1 for temporally integrated compared to masked reports. Interestingly, we found the same effect for the metacontrast masking task in which temporally integrated percepts showed a more negative N1 compared to masked reports. Accordingly, an individual variable masking mechanism may have resulted in the same shift of the PSE in both tasks. In the end, however, this N1 effect was only marginally significant for both tasks. My suggestion that established temporal paradigms are confounded by a masking mechanism should hence be treated with caution. To further investigate this potential masking confound, I plan on determining trials in the missing element task for which masking would be especially likely, for example in cases in which some elements of the first grid are surrounded by elements of the second the grid. These trials should show an especially low N1 and hence indicate a masking mechanism.

3.4 Limitations and future research

Our third study was designed to not only investigate ERP differences but also pre-stimulus phase and power differences. Due to methodological issues, the analysis of our phase effects will finish after the submission of this thesis. However, the current state of the phase and power analysis is presented in the supplements of our third study (*Appendix III - manuscript for study 3*). The final phase results will give us more insights into the relationship between temporal and masking mechanisms and provide us with more effects to investigate the degree of shared temporal (or masking) mechanisms between the metacontrast masking, the missing element and the two-flash task. Pre-stimulus phase differences have been associated with both temporal and masking effects and have been explained similarly to result from periodic variations in the neural excitability due to neural oscillations. Lately, this explanation has been questioned since it hypothesizes an interaction between phase and power effects which, however, could not be demonstrated in a two-flash task (Milton & Pleydell-Pearce, 2016). The data of our third study will also be able to investigate this hypothesized interaction for all of our three investigated paradigms. These findings will provide us with further evidence to either interpret pre-stimulus phase effects as periodic variations in the neural excitability or alternatively as fundamental patterns of our neural communication that affect our temporal processing (Milton & Pleydell-Pearce, 2016).

To analyze our phase data, we calculated in each of our studies the phase opposition sum (POS). The POS was proposed to be one of the best suited measures to investigate phase shifts between two and more report categories (VanRullen, 2016b). To calculate the POS, the inter-trial coherences of phase states in each report category are summed and then corrected by the overall inter-trial coherence (ITC). Accordingly, high POS values result if phase states are (1) similar to each other in each report category but (2) different from each other between report categories. There are several disadvantages to this measure that render its analysis and interpretation difficult.

First, the POS summarizes the phase states and their difference between report categories into one value. In addition, the POS always deviates positively from zero since the ITC ranges between 0 and 2. Thus, when performing inference statistical analyses, a comparison of the POS against zero would be too liberal while a comparison of the phase states between report categories is not possible. An inferential statistical analysis of the POS therefore needs a permutation procedure.

Second, the total size of the POS (or ITC) depends on the number of trials that are used to calculate it. For this reason, the number of trials in each report category needs to be equalized before performing any inferential statistics between report categories. As a result, only a subset of trials is extracted from the report category with more trials while the remaining trials are discarded. Since trials are extracted by chance, the resulting subset may be biased and may not reflect the original data basis. Although we performed a trial equalization in each of our studies, this effect can still be observed between paradigms in our third study (see figure S1 in the supplements of *Appendix III - manuscript for study 3*). Here, the missing element and two-flash task demonstrate much lower descriptive POS values since more trials were used to calculate them compared to the POS values of the metacontrast masking task. Moreover, since a trial equalization is only applied separately for each participant, POS values of participants with less trials per report category are larger than that of participants with more trials per report category. Accordingly, participants with less trials per report category will have are larger impact on the participant average. Against this background, it may be appropriate to also equalize trials between participants which, however, would entail the removal of even more trials.

Third, the POS can be easily misinterpreted to contain more information than it actually provides. Ultimately, the POS reflects a difference in phase states between report categories but the origin of this difference remains unknown.

Based on the assumption of temporal integration windows, phase differences are often interpreted to reflect that one phase interval is associated with a temporal integration while the opposite phase interval is associated with a temporal segregation. As a result, an implicit antagonism between temporal integration and segregation is created: either two stimuli fall into the same or different temporal integration windows but in each case, they are temporally processed. However, significant POS values can also result if one report category is associated with a specific phase interval and the other one not. Let us assume that a temporally integrated percept is associated with a specific phase interval but a temporally segregated percept is not. Accordingly, the pool of all trials consists of the same amount of trials with a temporally integrated and segregated percept and phase states will likely be evenly distributed. The extraction of trials with a temporally integrated percept from the pool of all trials will extract all those trials that depict a phase state in a specific phase interval while it will leave all the other trials that show on average an opposite phase state. However, this opposite phase state is only created artificially by trials that are not associated with a temporally integrated percept which does not necessarily reflect an association with a temporally segregated percept. Accordingly, the POS does not inform us that a specific percept is associated with a specific phase state and most importantly, does not automatically implicate an antagonistic relationship between two mechanisms. In the end, a significant POS between temporally integrated and segregated percepts may result from (1) temporally integrated percepts but not temporally segregated percepts being associated with a specific phase interval, (2) temporally segregated percepts but not temporally integrated percepts being associated with a specific phase interval or (3) temporally integrated and segregated percepts being associated with opposite phase intervals. While it would be possible for temporal integration and segregation to be independent in (1) and (2) they would have an antagonistic relationship in (3). Accordingly, the POS is not suited to investigate the (in-)dependence of temporal integration and segregation.

To investigate the temporal and masking mechanisms in the metacontrast masking paradigm, we utilized a phenomenological approach and asked participants in each trial to categorize their perceptual impression. Phenomenological approaches have been utilized in the metacontrast masking paradigm before (Reeves, 1982), and produced data that were correlated to that of performance-based approaches (Koster et al., 2020). We further validate the phenomenological approach by replicating the neural correlates of both temporal and masking mechanisms in a metacontrast masking paradigm. Hence, although our phenomenological may suffer from our participants' response biases they do not render our data inconclusive (Nisbett, 1977; Vermersch, 1999; Velmans, 2007) but enable us to measure qualitative differences in our phenomenal perception that change fast between trials.

Demonstrating the presence of the neural correlates of temporal mechanisms in the metacontrast masking paradigm requests a rethinking of how to determine the neural correlates of masking. Without a differentiation of unmasked trials into trials with a temporally integrated or segregated percept, a comparison of the neural activity between unmasked and masked trials could reflect both temporal and masking mechanisms. Such a differentiation allowed us to associate the masked percept with a spatio-temporal process since both the masked and temporally integrated percepts showed the same neural effect when compared against the temporally segregated percept. Since performance-based approaches are ill-suited to differentiate between such qualitative different phenomenal impressions, I want to further promote the usage of the phenomenological approach to further investigate temporal and masking mechanisms in the metacontrast masking paradigm.

In the near future, the investigation of temporal and masking mechanisms in the metacontrast masking paradigm has the potential to become more complex. Although we have questioned Reeves' (1982) dual process theory of metacontrast masking, his assumption that temporal integration and segregation constitute two independent mechanisms may still be true. Currently unpublished data from one of our metacontrast masking tasks indicated that participants report to sometimes perceive both a temporally integrated and segregated percept of the target-mask sequence in the same trial. This mixed percept could be used to identify the neural correlates specifically for either temporal integration or segregation by comparing the neural activity between the pure and the mixed percept. For example, by comparing the neural activity between temporally integrated and the mixed percept, the remaining activity difference could be associated with mechanisms that are associated with a temporally segregated percept.

In addition, participants report to sometimes perceive a temporally segregated percept in which the target is not visible. Interestingly, participants report such a percept and describe it as either (1) a “feeling” that there was a second event despite not perceiving it visually or (2) the perception of two consecutives masks despite that only one mask is presented in each trial. Since we have been aware of this percept before conducting our third study, we allowed our participants to report it. For now, however, we did not differentiate between those and a masked percept. It would be interesting to investigate whether a neural comparison of an *unmasked* temporally integrated and segregated percept is similar to the comparison of a *masked* temporally integrated and segregated percept.

3.5 Conclusion

This dissertation constitutes one of the first steps towards a fusion of the temporal and masking research. In our three studies, we demonstrated for the first time the neural correlates of temporal mechanisms in a metacontrast masking paradigm and hence support models and theories that propose multiple (temporal) mechanisms to contribute to the masking phenomenon. Specifically, we found both the pre-stimulus phase in the theta, alpha and beta frequency band to differ between a temporally integrated and segregated perception of the target-mask sequence. While we associated theta and alpha phase differences with a bottom-up temporal mechanism in the ventral stream, we associated beta phase differences with a top-down biasing mechanism in frontal areas that affects temporal processing further down in the neural hierarchy. In addition, our post-stimulus ERP differences indicated a spatio-temporal integration mechanism to be relevant for both a temporally integrated and a masked perception of the target-mask sequence. This direct relationship between temporal and masking mechanisms is hard to be aligned with theories and models that propose an independence of these mechanisms but exemplify the potential information gain that a concurrent investigation of temporal and masking mechanisms can provide.

Unravelling the (temporal) mechanisms that contribute to the masking phenomenon is essential since the masking paradigm is utilized in a variety of different research fields, inter alia to investigate one of the most pressing questions in neuroscience today: the consciousness phenomenon. However, not only the masking research would benefit from considering temporal mechanism since our findings indicated a potential masking confound in established temporal paradigms. Overall, our findings offer a multitude of interesting pathways to continue the quest of building a bridge between the temporal and masking research. The most pressing next questions will likely be (1) whether temporal integration and segregation constitute independent mechanisms and if so how they each relate to the masking phenomenon and (2) whether pre-stimulus phase differences in both temporal and masking studies reflect a periodic variation in the neural excitability due to neural oscillations.

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Appendix I - manuscript for study 1

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Manuscript title

Neural correlates of temporal integration and segregation in metacontrast masking: a phenomenological study

Short title

Temporal processing in metacontrast masking

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Abstract

Temporal integration and segregation have been investigated in both the research on the temporal mechanisms in visual perception and in research on visual masking. Although both research lines share theoretical, methodological and empirical similarities there is little overlap between them and their models of temporal processing are incompatible. As a first step towards the unification of both lines of research, we investigated the electrophysiological correlates of temporal integration and segregation in a metacontrast masking paradigm. Participants reported in each trial whether they perceived the target-mask sequence as a simultaneous or temporally segregated percept while their EEG was recorded. A comparison of both temporal report categories resulted in an ERP difference after stimulus presentation (200 to 450 ms) that closely resembles the contour integration negativity. Moreover, we found that phase states were shifted between perceptual report categories in the alpha (450 to 250 ms) and beta (225 to 125 ms) frequency band before stimulus presentation and induced a sinusoidal periodicity in later temporal report proportions. Thus, we show that neural correlates of temporal integration and segregation can be generalized to metacontrast masking. These findings emphasize the potential role of temporal mechanisms in the emergence of the masking phenomenon. Additionally, our findings validate our phenomenal approach by demonstrating similar neural correlates of temporal integration and segregation as in performance-based tasks. Future research may profit from our phenomenal approach to disentangle the (neural) interplay between temporal and masking mechanisms.

1. Introduction

Intuitively, we perceive our constantly changing and dynamic surroundings as a continuously flowing stream of events in which the present is perfectly separable from the past and future. However, successive events can be erroneously perceived simultaneously if they happen close enough in time (Exner, 1875; Hogben & Di Lollo, 1974). This phenomenon is as old as the thaumatrope: a child's toy from the 18th century in which a disc is rotated so fast that the pictures on both sides of it (e.g. a bird on one side and a cage on the other side) fuse perceptually together and appear simultaneously (a bird in a cage). Such findings suggest that our perception has a limited temporal resolution that allows for the creation of only a few perceptual moments per second (Stroud, 1956; VanRullen & Koch, 2003; Block, 2014; VanRullen, 2016a) and thus contradicts the idea of a continuous stream of perception.

A perceptual moment may be determined by a temporal integration window: a time window in neural processing that favors the combined processing of successive events (Varela, Toro, John, & Schwartz, 1981*;* Pöppel, 1997; VanRullen & Koch, 2003; Hanslmayr, Volberg, Wimber, Dalal, & Greenle, 2013; Jensen, Gips, Bergmann, & Bonnefond, 2014). A simple account of temporal integration windows allows for two possibilities: successive events either occur in the same temporal integration window and are temporally integrated, or they occur in different temporal integration windows and are temporally segregated. According to this view, temporal integration and segregation should depend on each other and should constitute the antagonistic expressions of one underlying temporal process: if events are not temporally integrated, they are segregated and vice versa. In contrast to such an antagonistic view, several accounts of visual masking propose temporal integration and segregation to be independent processes (Reeves, 1982; Albrecht & Mattler, 2016; Koster, Mattler, & Albrecht, 2020) thereby trying to explain the masking phenomenon.

1.1 Temporal integration and segregation in metacontrast masking

Metacontrast masking is a special form of visual backward masking in which the visibility of a visual target stimulus is reduced by the subsequent presentation of a visual masking stimulus (Breitmeyer & Ögmen, 2006). Crucially, the masking stimulus fits snugly around the target contours, but does not overlap with it. Under these conditions, target visibility varies as a function of the stimulus onset asynchrony (SOA) between target and mask. Typically, this masking function is U-shaped with the lowest target visibility at intermediate SOA. In many cases, participants report to not have seen the target at all (e.g., Werner, 1935; Koster et al. 2020). According to the dual process theory of metacontrast (Reeves, 1982), this is the result of the target being neither temporally integrated with nor segregated from the mask. Here, temporal integration and segregation are handled as independent, dissociable processes that are protecting the target from masking. Whereas the strength of the temporal integration process is strongest in short SOA and continuously declines with increasing SOA, the strength of the temporal segregation process is weakest at short SOA and continuously increases with increasing SOA. Consequently, both temporal processes are equally weak at intermediate SOA and the likelihood of the target being neither successfully temporally integrated nor segregated is at its maximum, which results in the typical U-shaped masking function. In line with this approach there is ample evidence that perceptual contents can differ between short and long SOA (Neumann &

Scharlau, 2006; Albrecht & Mattler, 2012; Jannati & Di Lollo, 2012; Sackur, 2013; Koster et al., 2020). Participants report to perceive the target simultaneously with the mask especially at short SOA whereas target and mask are typically perceived successively at long SOA (e.g. Werner, 1935; Reeves, 1982; Koster et al., 2020). These phenomenological reports have been shown to correlate with objective performance in discrimination and detection tasks (Reeves, 1982; Koster et al. 2020).

1.2 Unifying temporal and masking paradigms

There is little overlap between the research on visual masking and the research on the temporal mechanisms in visual perception although the same processes are investigated and their experimental paradigms share many similarities (e.g., presenting two brief successive stimuli with a temporal delay of up to 100 ms). On the contrary, their models of temporal integration and segregation as (1) the antagonistic expressions of one underlying process or as (2) two independent processes are hardly to be reconciled with each other. A unification of both lines of research would be able to shed light on this theoretical incompatibility on the long run and allow for each line of research to profit from one another. On the one side, although the role of temporal integration and segregation has been investigated behaviorally in masking before (Reeves, 1982; Koster et al., 2020; Francis & Cho, 2008), neural evidence is sparse to date. On the other side, although several neural correlates of temporal integration and segregation have been proposed using temporal paradigms, the role of masking processes in these paradigms have not been systematically investigated to date (see for example Wutz, Weisz, Braun, & Melcher, 2014; Akyürek & Wijinia, 2019).

Common paradigms for studying temporal mechanisms are, for example, various forms of the missing element task to investigate temporal integration mechanisms (e.g., Hogben & Di Lollo, 1974; Akyürek, Schubö, & Hommel, 2010; Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016; Wutz, Melcher, & Samaha, 2018) or the two-flash task to investigate temporal segregation mechanisms (e.g., Samaha & Postle, 2015; Milton & Pleydell-Pearce, 2016; Ronconi, Oosterhof, Bonmassar, & Melcher, 2017). In each of these paradigms, two events are presented in quick succession and a successful or a failed temporal integration (or segregation) is inferred by objective performance in a perceptual task. The rationale behind these paradigms is that a correct response necessarily requires a successful integration (or segregation) and that in contrast, an incorrect response reflects a failed integration (or segregation).

A shortcoming of performance-based measures is the strong assumption that the task cannot be accomplished by using perceptual cues other than a temporally integrated (or segregated) percept. To show good performance in integration tasks (e.g. the missing element task) both stimuli need to be perceived simultaneously and hence be successfully temporally integrated. In contrast, poor performance (i.e. failed integration) may be attributed to perceiving both stimuli temporally segregated but it may also be due to perceiving only the first or the second stimulus due to masking or inattention. This is also true for segregation tasks (e.g. the two-flash task), in which good performance demands the successive perception of two stimuli and hence a successful temporal segregation. In contrast, poor performance (i.e. failed segregation) may be attributed to perceiving both stimuli temporally integrated but it may also be due to perceiving only the first or the second stimulus due to masking or inattention.

Recently, a modified version of the missing element paradigm has been introduced that allows for the combined investigation of temporal integration and segregation by changing the task at hand (missing element task vs. odd element task) while keeping the stimulation stable (e.g. Wutz et al., 2016; Wutz et al., 2018). Thereby, temporal integration and segregation processes can be investigated in a unified paradigm with similar attentional requirements and task difficulties. A good performance in the odd element task requires the perception of one stimulus (i.e. a non-integrated percept), and thus, may result from either perceiving two successive events or from the second stimulus masking the first (or the other way around). In sum, while using any paradigm that is based on objective task performance, a comparison of trials with a successful and failed temporal integration (or segregation) may not reflect differences in temporal processing (alone) but may also represent a comparison of masked and unmasked trials.

1.3 Neural correlates of temporal integration, segregation and masking

The possibility of a masking confound in temporal paradigms poses the questions whether their neural correlates really reflect temporal mechanisms and whether they would also show in the absence of a masking confound. This question is especially important since the proposed neural correlates of temporal and masking mechanisms share many similarities.

Before stimulus presentation, phase states especially in the alpha and theta frequency bands have been demonstrated to differ between trials with a successful and a failed temporal integration (or segregation; Varela et al., 1981; Milton & Pleydell-Pearce, 2016; VanRullen, 2016a; Wutz et al., 2016; Ronconi et al., 2017). These lower neural frequencies have been proposed to temporally orchestrate neural processing by periodically varying the excitability of the underlying neural substrate (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Jensen et al., 2014; VanRullen, 2016a). Whereas the crests of a neural frequency inhibit the underlying neural processing, its troughs allow for an uninhibited neural processing. Intervals of uninhibited neural processing may result in the formation of a temporal integration window whereas intervals of inhibited neural processing may separate temporal integration windows from each other. In this framework, one phase state would be associated with the maximum likelihood of a temporal integration whereas the opposing phase state would be associated with the maximum likelihood of temporal segregation. This observation is the cradle for the idea that temporal integration and segregation are the two antagonistic expressions of one underlying process that is reflected in the phase state of lower neural frequencies. In this way, a failed temporal integration would automatically imply a successful temporal segregation and vice versa. A similar phase dependency has also been demonstrated in metacontrast masking in which the phase states in the lower frequency bands differ between unmasked and masked trials (Mathewson et al., 2009). The periodically varying excitability of the underlying neural substrate does also function here as an explanation of the results: Unmasked percepts were especially reported when the target was presented in the trough of lower neural frequencies and the target was hence processed in the most excitable phase state.

Apart from phase differences, it has been demonstrated that the power in the beta frequency band before stimulus presentation is more pronounced for trials with a successful compared to a failed temporal integration (Geerligs & Akyürek, 2012; Wutz et al., 2014), possibly reflecting the readiness of the visual system to temporally integrate subsequently presented visual stimuli (Geerligs & Akyürek, 2012). An increased beta power (Schubert, Haufe, Blankenburg, Villringer, & Curio, 2009) as well as a decreased alpha power (Mathewson et al., 2009) have also been reported for the comparison of unmasked to masked trials.

In the time window after stimulus presentation, trials with a successful compared to a failed temporal integration have been demonstrated to show a more negative ERP in early time windows (N1, N2 and early P3) and a more positive ERP in later time windows (late P3; Akyürek et al., 2010). Based on differences in the N1 component the authors concluded that temporal integration already occurs early in visual processing thereby affecting consecutive processes like spatial integration (reflected in the N2 and early P3) and memory consolidation (reflected in the late P3). Note, that a more negative N1 component has also been associated with a successful temporal segregation in a two-flash task (Ronconi et al., 2017). ERP differences within a similar time window have been demonstrated for metacontrast masking in which unmasked compared to masked trials show a greater negativity in earlier time windows termed the visual awareness negativity (VAN) and a greater positivity in later time windows termed the late positivity (LP; Railo, Koivisto & Revonsuo, 2011).

1.4 A phenomenal task to investigate temporal integration and segregation

As a first step towards the unification of these different lines of research, we investigated the neural correlates of temporal integration and segregation using a metacontrast masking paradigm. In each trial we asked our participants to report whether they perceived the target-mask sequence as a simultaneous, temporally segregated or masked percept while their EEG was recorded. This phenomenological approach provided us with a direct measure of the temporal content arising in each trial whereby simultaneous and temporally segregated reports only differed with respect to the temporal course of the target-mask sequence. Consequently, solely masked reports should be associated with attentional and masking processes and a comparison of simultaneous and temporally segregated reports should exclusively reflect differences in temporal processing.

Keeping stimulus presentation parameters constant for each participant, electrophysiological analyses contrasted trials with a simultaneous (temporal integration) and temporally segregated (temporal segregation) perception. We expected to find phase and power differences before and ERP differences after stimulus presentation. Replicating the neural correlates of temporal integration and segregation from studies using more typical paradigms (e.g. missing element task or two-flash task) would not only support the relevance of temporal processes in metacontrast masking but also demonstrate that they are not the result of a masking confound.

2. Method

2.1 Participants

34 students from the Georg-August-University Göttingen participated for course credit compensation. Prior to the experiment all participants gave their informed consent. Six participants were excluded from all analyses because of technical failures ($n = 1$), dropout after the first session ($n = 2$) or an insufficient quality of behavioral data fits ($n = 3$). For the electrophysiological analyses, additional 13 participants needed to be excluded because of too few trials in at least

one temporal report category. Thus, 15 participants (13 female, 2 male) between 19 and 29 years old (*M* = 21.7, *SD* = 2.8) were included in the electrophysiological analyses. All participants reported to have normal or corrected to normal vision. One participant reported to be left handed.

2.2 Stimuli

The experiment was run on a 19” CRT monitor with a refresh rate of 100 Hz. Stimulus presentation was controlled by Presentation® (Version 18.0, Neurobehavioral Systems, Inc.). All stimuli were presented in black (0.03 cd/m^2) on a white background (103.6 cd/m^2) in the center of the screen. Target stimuli were filled squares and diamonds. The masking stimulus was an eight-pointed star which was constructed by overlaying a square and a diamond shape. Figure 1A depicts all stimuli and their sizes.

2.3 Task

Participants were presented with target-mask sequences as shown in figure 1B and had to report the perceived temporal succession of target and mask in a three-choice task. They indicated by button press if they perceived both stimuli as a simultaneous, temporally segregated or masked percept. At the beginning of the experiment they were thoroughly informed about these response categories. A s*imultaneous* perception should be reported if some visual feature of the target was perceivable inside of the white space of the mask. A temporally *segregated* perception should be reported if some visual feature of the target was perceived before the mask and the white space of the mask stayed empty. The m*ask only* perception should be reported only if absolutely no visual feature of the target was perceived neither before nor inside of the mask. It was emphasized that the stimulus presentation would be so fast that a clear perception of the target would be not possible in most cases but that it would be sufficient to perceive only some visual feature of it (some blackish shadow, its edges, its contour, etc.) to either report *simultaneous* or *segregated*. If the target was both perceived inside (*simultaneous*) and before the mask (*segregated*) participants were instructed to report the most dominant perception. All reports were assigned to keys on the tabulator of the keyboard (1, 2 and 3). This assignment was counterbalanced over participants.

**** Insert figure 1 here ****

2.4 Procedure

The experiment consisted of two sessions which took place in the dimly lit EEG lab. EEG was recorded only in the second session. Participants were seated in a comfortable chair 100 cm from the screen. The trial sequence was identical for both sessions (figure 1B). Each trial started with the presentation of the fixation cross for 1000 ms, followed by a blank screen for 1000 ms to 1500 ms. Then the target was presented for 20 ms followed by the mask for 120 ms. The SOA between target and mask varied between 20 ms to 100 ms in steps of 10 ms. Following the mask, a blank screen was presented for 1000 ms before the rotated fixation cross informed participants that reports could be made. Participants responded without time limit but were instructed to evaluate their perceptions as spontaneously as possible. Each session comprised 720 trials organized into 16 blocks (first session) and 15 blocks (second session) respectively which took around 60 minutes. Target shape (square/diamond) and SOA varied pseudo-randomly in each block.

The first session was used to determine one SOA for each participant for which *simultaneous* and *segregated* reports occurred with equal proportions. This *primary SOA* was presented in the second session on half of all trials to get as many trials with varying perceptual reports but stable physical stimulation as possible. All other SOAs were presented with equal proportions in the other half of all trials. To check whether participants memorized the correct perceptual criteria (and to correct them if needed) participants had to describe their perceptual criteria after the second block of the first session, before beginning the task in the second session and in the end of each session. Each participant's resting EEG was recorded continuously for two minutes with eyes closed at the end of the second session to allow for the extraction of the individual alpha frequency (see supplements, section 1).

2.5 Data analyses

2.5.1 Behavioral data

For the data of the first session, proportions of each report category were calculated separately for each participant and SOA. Proportions of *simultaneous* and *segregated* reports were fitted by a cumulative normal distribution using the *Palamedes* toolbox (Prins & Kingdom, 2009) for *MATLAB* (MATLAB 9.4; MathWorks). Parameters for the point of subjective equality, the slope of the curve as well as the guessing rate and lapse rate were allowed to vary. The SOA closest to the intersection of both functions was used as *primary SOA* in the second session. Three participants were excluded from further analyses because the fitted functions either did not intersect, the function for *simultaneous* reports increased over the SOA or the function of *segregated* reports decreased over the SOA.

Only trials with a *primary SOA* presentation were investigated in the electrophysiological analyses. In this way, physical stimulation could be kept stable for each participant but not over participants since the *primary SOA* had to be determined for each participant separately. Further participants were excluded from the main analyses if they did not give *simultaneous* and *segregated* reports each in at least 50 trials that used their *primary SOA*. 13 participants were affected by this exclusion criterion. For the remaining 15 participants the amount of trials in each report category was equalized by randomly drawing as many trials from the report category with more trials as there were in the report category with less trials. Trials with an *only mask* report were not included in any analysis. In the end, between 54 and 141 trials for each the *simultaneous* and *segregated* report category ($M = 97.2$, $SD = 28.6$) were forwarded to the main analyses for each participant.

2.5.2 Electrophysiological data

EEG was recorded using a Biosemi ActiveTwo system with 64 electrodes placed according to the extended 10-20 system on the scalp. Additional electrodes were placed on the outer canthi of both eyes, under the left eye and on both mastoids. The data were recorded with a sampling frequency of 512 Hz and offline re-referenced to the linked mastoids. Electrode offsets were at a maximum of ± 20 mV. All data were preprocessed and analyzed using the toolboxes EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014) and custom-built MATLAB code. Data were bandpass filtered between 0.1 Hz and

50 Hz (IIR Butterworth filter, 12 dB/octave) and segmented into epochs from -1000 ms to 1000 ms relative to target onset. Epochs with large motor artifacts were discarded by visual inspection. Ocular artifacts were corrected using independent component analysis (Jung et al., 2000). Afterwards, epochs were once again visually inspected for remaining artefacts. On average 14.5% trials (*SD* = 12.1%) were excluded.

Event-related potentials (ERP) were calculated for each report category between -200 to 1000 ms around target onset and baseline corrected using the pre-target time interval. Power and phase data were computed by means of a continuous wavelet transform for frequencies ranging from 2 to 35 Hz in steps of 1 Hz, and time intervals ranging from 500 to 0 ms before target onset in steps of 10 ms. The number of cycles was increased for higher frequencies to counter differences in frequency precision between higher and lower frequencies (2 Hz: 1, 3-4 Hz: 2, 5-6 Hz: 3, 7-9 Hz: 4, 10-12 Hz: 5, 13-19 Hz: 6, 20-29 Hz: 7, 30-35 Hz: 8).

Two different baselines were applied to the power data. Each baseline was calculated as the average power in the whole time window before stimulus presentation separately for each frequency. A condition-average baseline was calculated by additionally averaging the baseline over conditions. Applying this condition-average baseline retains all condition differences both absolute as well as phasic differences. A condition-specific baseline was calculated separately for each condition. Applying this condition-specific baseline eliminates all absolute condition differences but retains phasic differences. By applying each baseline, absolute power differences can be separated from phasic power differences (see e.g. Cohen, 2014).

To evaluate phase differences between temporal report categories the phase opposition sum (POS) was calculated (VanRullen, 2016b). For this purpose, the inter-trial coherence (ITC) of trials with (1) only *simultaneous* reports, (2) only *segregated* reports and (3) *simultaneous* and *segregated* reports were related to each other according to the following formula:

$$\mathrm{POS} = \mathrm{ITC}_{\mathrm{Simultaneous}} + \mathrm{ITC}_{\mathrm{Segregated}} - 2 * \mathrm{ITC}_{\mathrm{Simultaneous\ \&\ Segregated}}$$

The ITC reflects how well phase states of a report category align to each other and ranges from 0 (no phase coherence at all) to 1 (perfect phase coherence) thereby resulting in POS values ranging from 0 to 2. High POS values result from high phase coherences in each report category and a phase shift in between of them.

2.5.3 Statistical analyses

ERP, power and POS data were analyzed using nonparametric cluster-based permutation tests including all channels (64), time points (ERP: 0 to 1000 ms after target onset; POS/power: 500 to 0 ms before target onset) and frequencies (ERP: not used; POS/power: 2 to 35 Hz).

For the power and ERP data, we applied the analysis procedure reported in Maris and Oostenveld (2009). To determine the significance of individual channel-time-frequency combinations, t values were calculated by comparing the data of *simultaneous* against those of *segregated* reports. All directly neighboring significant (two-sided) channel-time-frequency combinations were clustered and their t values summed. To evaluate the significance of each cluster, its cluster t sum was compared to a distribution of cluster t sums under a null effect. To generate this distribution, participant averages were randomly assigned to each report category and then all previous steps were repeated. For each analysis, only the largest cluster t sum was extracted. We systematically performed all possible trial assignments resulting in a distribution of 32 768 (2^{15}) cluster t sums. The upper 5th percentile of this null distribution was used as a threshold for cluster significance.

For the POS, we needed to apply a different procedure since first, the POS already integrates the two report categories into one value (hence a comparison between report categories is not possible anymore) and second, the POS is always greater than 0 resulting in an overestimation of effects when compared against it (VanRullen, 2016b). Therefore, we applied the resampling procedure described in Busch, Dubois and VanRullen (2009) and combined it with the clustering procedure described in Maris and Oostenveld (2009). To determine the significance of individual channel-time-frequency combinations, trials were randomly assigned to each report category and the POS was calculated. This was repeated for 1000 times resulting for each participant in a distribution of POS values that would have resulted from reporting at random. A random POS value was then drawn from this distribution for each participant and a grand average was calculated. This was repeated for 100 000 times resulting in a null distribution of POS values. For each channel-time-frequency combination, the upper 5th percentile of this null distribution was used as a significance threshold (one-sided). Next, all directly neighboring significant channel-time-frequency combinations were clustered and their POS values summed. To evaluate the significance of each cluster, its cluster POS sum was compared to a distribution of cluster POS sums under a null effect. To generate this distribution, we extracted the largest cluster POS sum from each of the 100 000 individual datasets that make up the null distribution. The upper 5th percentile of this distribution of cluster POS sums was used as a threshold for cluster significance.

2.5.4 Phase induced behavioral periodicity

To characterize significant phase effects on the individual level, we investigated the influence of phase states before stimulus presentation on later temporal reports separately for each participant. To do so, we determined first the center time-frequency point of each significant cluster in the POS analysis and then the electrode with the highest POS in it. For this electrode and time-frequency point, we calculated the corresponding phase states in all trials. A moving window with a length of $\pi/2$ sorted the phase states into 360 overlapping bins. For each step of the moving window, the proportion of trials with a *simultaneous* report was calculated. Since only *simultaneous* and *segregated* reports were considered for this analysis, *segregated* report proportions resulted from 1 minus the *simultaneous* report proportion. To assess the degree of behavioral periodicity, *simultaneous* report proportions were fitted with a sine wave as a function of phase state. Whereas the frequency parameter was fixed to 1 and the intercept parameter to .5, the amplitude and phase offset parameters were left free to vary. The sine wave's amplitude served as an indicator of the amount of periodicity that the phase state elicited in the temporal report proportions. To assess the significance of amplitudes, a distribution of amplitudes under the assumption of null effects was generated by randomly assigning trials to either temporal report category for 1000 times. The upper 5th percentile of the resulting distribution was used as a significance threshold.

3. Results

3.1 Behavioral data

Figure 2 depicts proportions of each report category for both individual and averaged data. In each session, the proportion of *simultaneous* reports decreased and that of *segregated* reports increased as a function of the SOA. In contrast, *only mask* reports showed a reversed-U-shaped function over the SOA. Linear and quadratic trends were significant for each report category and session (see table S2 in the supplements). Though this overall data pattern is present in all participants, individual data courses varied substantially. Participants especially differ in the overall proportion of *only mask* reports ($M = .17$, $SD = .12$, range = .05-.39) and their *primary SOA* ($M = 54.29$ ms, $SD = 12.30$ ms, range = 40-80 ms). In contrast to this high between-subject variability, the individual data patterns remain stable between sessions as shown by a high retest reliability of the *primary SOA* ($r(26) = .78$, $p < .001$, for all participants and $r(13) = .86$, $p < .001$ for participants that were included in the electrophysiological analyses).

**** Insert figure 2 here ****

3.2 Event-related potentials

A nonparametric cluster-based permutation test on all channels and time points after target onset (0 to 1000 ms) revealed a single significant cluster ($p = .027$) showing that *simultaneous* reports were associated with a more negative ERP amplitude than *segregated* reports (figure 3A). This cluster was restricted to the time interval between 200 to 450 ms after target onset and was especially present in centro-parietal electrodes. The effect first showed a centralized topography over the channel Cz but then split up into both hemispheres (figure 3B). A similar significant cluster (*p* = .011) also resulted from changing the onset of the ERP from target to mask onset (see figure S1 in the supplements).

**** Insert figure 3 here ****

3.3 Pre-stimulus power and phase effects

A nonparametric cluster-based permutation test was run for each the power and POS data by inserting all channels, all time points before target onset (500 to 0 ms) and all frequencies (2 to 35 Hz) into it. For the power data, there were no significant clusters (condition average baseline: *p* = .447, condition specific baseline: *p* = .572). For the POS, our analysis yielded one large significant cluster (*p* = .025), which can be separated into two sub-clusters each comprising more than 20 channels (figure 4). One sub-cluster was located in the alpha frequency range (7 to 14 Hz), comprised time points from 450 to 250 ms before target onset and showed a fronto-central topography. The other sub-cluster was located in the lower beta frequency range (15 to 20 Hz), comprised time points from 225 to 125 ms before target onset and showed a topography that was restricted to distal central channels in the right hemisphere and distal parieto-occipital channels in the left hemisphere. For each of these clusters and report categories figure 4B addtionally depicts the topographies of the ITC. By eye, the ITC of *simultaneous* reports tends to reflect the topography of the phase effect in the alpha frequency band whereas the ITC of *segregated* reports tends to reflect the topography of the phase effect in the beta frequency band. The average sub-cluster ITC, however, does not differ significantly between *simultaneous* and *segregated* reports neither in the alpha ($p = .228$) nor the beta sub-cluster ($p = .134$) when tested with a nonparametric cluster-based permutation test (Maris & Oostenveld, 2009).

**** Insert figure 4 here ****

To elaborate more on these phase differences on the individual level, figure 5 depicts the proportion of *simultaneous* reports as a function of the phase state in the center of each sub- cluster in the POS analysis (alpha: -330 ms, 8 Hz, AF7; beta: -220 ms, 18 Hz, CP4.). For both the alpha and beta sub-cluster centers, sine wave fits to the data resulted on average in good fitting scores as well as significantly higher amplitudes than would have been expected from chance (alpha: $RMSE = .039$, $p = .004$; beta: $RMSE = .045$, $p = .017$). Thus, phase states before stimulus presentation induced a considerable sinusoidal periodicity in later temporal report proportions.

**** Insert figure 5 here ****

3.4 Additional analyses

To investigate whether our effects are limited to a sub-group of included participants, we performed all analyses with a significant effect once again but with a more liberal inclusion criterion of at least 20 reports for each a temporal integration or segregation made in the primary SOA. As a consequence, 24 participants were included in the additional data analysis. Though 20 trials cannot provide a reliable estimate for a participant's average ERP or POS and are hence rendering all effects insignificant, the descriptive results are comparable to those in our main analysis (see figure S2 in the supplements for the ERP effect and figure S3 in the supplements for the POS effect). While the ERP effect depicted a more occipital topography, the POS effect was more pronounced in the beta and less pronounced in the alpha sub-cluster. In sum, these results indicate that the effects of our main analysis are robust and not an artefact of a low sample size.

4. Discussion

Though the research on masking in visual perception and the research on the temporal mechanisms in visual perception share theoretical, methodological and empirical similarities, there has been almost no overlap between them. Our study presents a first step towards the unification of both lines of research by comparing reports of temporally integrated to reports of temporally segregated percepts in a metacontrast masking paradigm while excluding reports of masked percepts from all analyses. A comparison of temporally integrated and segregated reports resulted in an ERP difference from 200 to 450 ms after stimulus presentation showing more negative amplitudes for the integrated compared to the segregated reports. Additionally, phase states differed in the alpha and beta frequency band before stimulus presentation when comparing the temporally integrated to segregated reports. These phase differences induced a sinusoidal periodicity in later temporal report proportions.

4.1 Temporal integration and segregation occur in metacontrast masking

Our behavioral results replicate findings of former metacontrast masking studies that also used phenomenal reports and found the proportion of temporally integrated reports to decrease, that of temporally segregated reports to increase and, that of mask only reports to show an inversed U-shaped function across the SOA (Reeves, 1982; Koster et al., 2020). This lends further evidence to the observation of qualitative differences between the perceptual contents arising at both ends of the masking function (Albrecht & Mattler, 2012; Jannati & Di Lollo, 2012; Sackur, 2013) and supports the notion that masking functions result from an interplay of multiple (temporal) processes (Reeves, 1982; Francis & Cho, 2008; Albrecht & Mattler, 2016; Koster et al., 2020). Albrecht and Mattler (2016) for example found two main factors that were associated with the individual target discrimination performance in short and long SOA, respectively. Our phenomenological findings support the authors' interpretation of these two factors as temporal processes, one that is associated with perceiving the target inside the mask in short SOA (temporal integration) and the other that is associated with perceiving the target temporally before the mask (temporal segregation). Against this background, individual differences in the masking function may be the result of participants differing in their ability to use or weigh temporal integration and segregation processes. In line with this reasoning, our findings show that participants substantially differ in the (primary) SOA that was needed to shift a temporally integrated to a temporally segregated perception of the stimulus sequence.

Differences in the phase state before stimulus presentation as well as in the ERPs after stimulus presentation replicate neural correlates of temporal integration and segregation and hence emphasize the role of temporal integration and segregation in metacontrast masking. In the ERP, we found a difference between 200 and 450 ms over centro-parietal channels showing more negative amplitudes for the temporally integrated compared to the segregated reports. The initial central topography of this effect expanded progressively into each hemisphere. This effect is strikingly similar to the contour integration negativity that results from comparing displays that either contain contours or randomly oriented line segments (Pitts & Martinez, 2014). Integrating or superimposing our target and mask stimuli results in white contours of (1) the small gap in between both stimuli as well as (2) four small triangles (see figure 1A). These contours do not occur, when both stimuli are perceived in succession. Thus, it is plausible that contour integration processes may be more engaged alongside a successful temporal integration of the target-mask sequence compared to a successful temporal segregation. Similarly, Akyürek et al. (2010) reported a greater negativity in the N1, N2 and early P3 time window for trials with a successful compared to a failed temporal integration in the missing element task. The authors interpreted this effect as an increased effort of spatial integration acting upon the already temporally integrated displays. Both this effect and the one found in our study show similar topographies and time courses, although the effect in Akyürek et al. (2010) starts earlier. This difference may be due to different stimulus configurations and task demands in both studies. It is also possible that the early effect in the N1 may (at least partially) be a more unspecific effect of good task performance and/or spatial attention. For instance, higher N1 amplitudes are usually observed for stimuli at attended locations (e.g. Luck et al., 1994) and have also been reported for trials with a successful compared to a failed temporal segregation in the two-flash task (Ronconi et al., 2017).

Before stimulus presentation, we found phase differences between trials with a temporally integrated and segregated report both in the alpha and beta frequency band. Phase differences especially in the alpha frequency band have been associated with temporal processing and the placement of temporal integration windows (Varela et al., 1981; Milton & Pleydell-Pearce, 2016; VanRullen, 2016a; Ronconi & Melcher, 2017; Ronconi et al., 2017; Battaglini et al., 2020; Herzog, Drissi-Daoudi, & Doerig, 2020). Though beta phase differences have only rarely been associated with temporal processing in the visual domain, they were associated with the temporal processing of somatosensory information (Baumgarten, Schnitzler & Lange, 2015), predictive timing in the auditory domain (Fujioka, Trainer, Large & Ross, 2012; Arnal, Doelling & Poeppel, 2015) and the top-down control of cognitive processes overall (Engel & Fries, 2010). One might speculate that the formation of temporal integration windows is not limited to lower frequency bands but can also take place in slightly higher frequencies opening up the possibility of multiple temporal integration windows working in parallel. Additionally, we found phase states both in the alpha and beta frequency band to elicit a sinusoidal periodicity in the proportion of later temporal reports. Such a behavioral periodicity has been reported before in the two-flash task (Ronconi & Melcher, 2017) and is in line with the idea of temporal integration windows in our neural processing since certain segments of a phase cycle favor a temporal integration whereas others favor a temporal segregation. Accordingly, the report proportions transition slowly and steadily from being beneficial for a temporal integration at one phase state to the opposite phase state that is beneficial for a later temporal segregation. Though most participants show this phase dependency its course is individual variable. At this point, we can only speculate why this is the case. It may be an artefact of extracting only the phase state of one specific frequency that on average depicts the frequency that carries the underlying temporal mechanism but actually differs between participants. It may also be that the temporal action that is associated with the respective phase states becomes relevant at different points in time for each participant.

Based on our findings, phase differences before stimulus presentation are associated with temporal processing even in the absence of a masking confound. However, this does not rule out the possibility that paradigms that are usually used to investigate temporal integration and segregation processes are confounded by a masking process. Oscillations in the time window before stimulus presentation have not only been reported to modulate the perceived timing of successive stimuli but also to affect the probability to perceive near-threshold or masked stimuli (e.g. Mathewson et al., 2009; Busch et al., 2009) leading to the possibility that the visibility of stimuli and their perceived timing share similar neural mechanisms (see e.g. VanRullen, 2016a). The mechanism of “pulsed inhibition” (Mathewson et al., 2009), that has been proposed to explain phase and power effects on the detection of near-threshold stimuli may also serve the function of temporally structuring neural processing (Jensen et al., 2014). Accordingly, the troughs of the alpha cycle, in which the neural substrate is especially excitable, would constitute temporal integration windows (Varela et al., 1981;

Milton & Pleydell-Pearce, 2016; VanRullen, 2016a). Phase differences in lower neural frequencies would hence be elicited by a comparison of both trials with a successful to a failed temporal integration (or segregation) as well as trials with an unmasked to a masked percept. Therefore, for paradigms in which both comparisons coincide, a masking confound may additionally boost differences in lower neural frequency bands. To our knowledge most of the current paradigms that use objective performance-based approaches to investigate temporal integration and segregation mechanisms are affected by this confound. A masking confound that boosts phase differences in lower neural frequency bands before stimulus presentation might explain why phase differences have been exclusively reported for lower neural frequencies to date but not higher neural frequencies like we do here. Future research that uses performance-based tasks to investigate temporal integration and segregation mechanisms should expand on the development of paradigms with which (1) both temporal integration and segregation can be investigated while keeping the physical stimulation stable (Wutz et al., 2016; Wutz et al., 2018) and (2) exclude masking confounds as an alternative explanation for their results. To this end, it might be useful to complement objective performance-based tasks with phenomenological measures to disentangle different subjective percepts.

4.2 Possible relations between temporal integration and segregation

According to Reeves' dual process theory (Reeves, 1982) temporal integration and segregation constitute two independent processes and masking results when both temporal integration and segregation fail at the same time. This assumption is hardly to be reconciled with temporal integration window models that propose temporal integration and segregation to constitute the two antagonistic expressions of the same underlying process.

Our phase difference data imply that one phase state was associated with a temporally integrated percept while an opposite (or shifted) phase state favored a temporally segregated percept. As a measure for the phase difference, we used the phase opposition sum which relies on (1) a phase difference between conditions and (2) the coherence of phases in both conditions. There are two possibilities of how reports of temporal integration and segregation could show opposite and coherent phase states. First, each report category benefits from opposite phase states. This would support the idea that temporal integration and segregation are the antagonistic expression of one underlying process. Second, only one report category benefits from a specific phase state. However, by taking out these trials from the pool of all trials, a lesser but still existing phase coherence around an opposite phase state is automatically induced in all remaining trials. This would support the idea that temporal integration and segregation are two independent or at least dissociable processes. A comparison of ITCs is thus a potential key to decide whether temporal integration and segregation are antagonistic (ITCs of equal size) or dissociable (ITCs of different size). Against this background, we want to stress the importance of analyzing not only the POS but also its underlying ITCs in future research. Descriptively, our data show that ITC difference. On the one hand, the topography of POS values in the alpha sub-cluster is mimicked by the ITC of trials with a temporally integrated report but not those with a temporally segregated report. On the other hand, the topography of POS values in the beta sub-cluster is mimicked by the ITC of trials with a temporally segregated report but not those with a temporally integrated report. These descriptive ITC differences, however, are not significant. Since these ITC differences can be expected to be quite low (despite their meaningfulness), our study may lack the power to fairly check for their significance.

4.3 Limitations and future research

Although we could demonstrate neural correlates of temporal processing before stimulus presentation in the phase state, we did not find meaningful power differences despite an increased beta power for trials with a successful compared to a failed temporal integration was reported before (Wutz et al., 2014; Geerligs & Akyürek, 2012). These studies differ from ours not only with regard to the paradigm, (phenomenological) task and measurement device but also with regard to the statistical analyses that they used. Since electrophysiological correlates of temporal processing have never before been investigated in the metacontrast masking paradigm, we have adopted a conservative approach in analyzing our data. Small power effects may have fallen victim to this increased difficulty of becoming significant. Therefore, it remains an open question for future studies whether the lack of power effects in our study is a methodological or statistical artifact. To exclude the possibility of inconsistent findings between studies to stem from different methodological and analyses protocols, multiple paradigms would have to be matched and investigated in the same study. This would allow for a reliable distinction between paradigm specific and general neural correlates of temporal processing.

Phenomenological approaches in which participants introspectively record and report their subjective perceptual experience have been criticized for yielding unreliable and unreproducible results because they are affected by, e.g., individual response criteria and biases and hence need to be interpreted with caution (Nisbett, 1977; Vermersch, 1999; Velmans, 2007). Though we cannot exclude a response bias in our phenomenal reports, we do not think that this renders our results inconclusive. First, reanalyzing our data by adding excluded participants and hence those participants with the (most likely) largest response bias into our sample resulted in similar descriptive findings as before. Second, we demonstrated that participants are able to reliably evaluate their perceptual experience since their behavioral pattern showed a high retest reliability between session one and session two. Third, our results are in line with findings from studies investigating the neural correlates of temporal integration and segregation using objective performance-based tasks. Koster et al. (2020) already demonstrated that in the very same metacontrast masking paradigm that we used, participants are able to generate comparable and reliable perceptual categories when asked to do so without having any prior guidance. These perceptual categories (of which we used three in the current study) are not made up but are correlated with the objective performance in discrimination and detection tasks (Reeves, 1982; Koster et al. 2020). An interesting next step would be to combine both report formats with each other and assess both objective discrimination performance as well as phenomenal reports on a trial by trial basis. There were mainly two reasons, why we refrained from such an approach. First, this would have rendered the task even more complicated. Second, we could not exclude that the decision on one task would inform the decision on the other task (e.g. reporting integration and segregation only if the shape of the target was clearly visible). Therefore, we did not want to draw the attention of the participants to the shape of the target but only to the temporal relation of target and mask. Overall, our findings support recent approaches that aim to systematically assess subjective experiences within a scientific framework (Dennett, 1991, 2003; Gallagher & Sørensen, 2006; Lutz, Lachaux, Martinerie, & Varela, 2002; Overgaard, 2004; Varela, 1996; Varela & Shear, 1999; Velmans, 2007). Such approaches allow for a differentiation between qualitatively different perceptual contents that may arise from trial to trial (e.g. Koster et al., 2020), which is difficult (if not impossible) to achieve with simple unidimensional scales (e.g. perception awareness scale; Ramsøy and Overgaard, 2004) or objective task performance. In sum, the present results contribute to the growing evidence that phenomenal measures can (and should) be considered as complementary and additional to objective performance measures in future behavioral and neurocognitive research.

Though the overall response pattern of participants remained the same over sessions, the primary SOA tended to shift slightly for some participants. As a consequence, 13 participants needed to be excluded from all further analyses since they had less than 50 reports with a temporal integration or segregation made in the primary SOA. Since we can demonstrate the same descriptive effects to result even when including a majority of the excluded participants, it is highly unlikely that our participant exclusion can account for our effects. Future studies using a similar paradigm may reduce this exclusion rate by determining the primary SOA shortly before presenting it predominantly.

We propose the paradigm that we developed in the current study and its phenomenological approach as a promising tool for future research to investigate the interplay of temporal integration, temporal segregation and masking in visual perception. The metacontrast masking paradigm may be especially well suited since the outcomes of temporal integration, temporal segregation and masking are each associated with a unique and comparably simple perceptual appearance. Future studies should aim to generate conditions in which all three perceptual appearances occur with approximately equal frequency and then contrast their electrophysiological activity. Including the masking reports into the analysis would break up the artificial antagonism that we induced in our study by only comparing temporally integrated and segregated reports against each other. This would provide the means to further investigate the (in-)dependence of temporal integration and segregation as well as their relationship to the masking phenomenon.

4.4 Conclusion

In conclusion, we found neural correlates of temporal integration and segregation in a metacontrast masking paradigm thereby supporting approaches that propose temporal processes to be integral for the emergence of the masking phenomenon. We made sure that a comparison of temporal integration and segregation was not confounded by other variables affecting task performance like masking by using a phenomenal task that allowed for the disentanglement of temporally integrated, temporally segregated and masked percepts. Since this entanglement and hence confound is present in most paradigms that use objective task performance, we recommend the further usage and development of phenomenal tasks which will eventually provide us with the means to investigate the (neural) interplay between temporal and masking mechanisms.

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Acknowledgments

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Figure Captions

Figure 1. (A) Depiction of the metacontrast masking stimuli and their sizes. The diamond target results from rotating the square target by 45°. (B) Schematic depiction of the experimental design. Target and mask were never presented simultaneously but always with a variable SOA in between of them. Whereas each SOA was presented with equal proportions in the first session, the primary SOA was presented in half of all trials in the second session. Participants' task was to report whether they perceived the target-mask sequence as either *simultaneous*, *segregated* or *mask only*. Participants responded without time limit.

Figure 2. Behavioral data of the first (A) and second (B) session. For each session, both the average (left) and individual data (right) are depicted. In each SOA proportions sum up to one. Error bars in the average data correspond to the between-subject standard deviation. The *primary SOA* is depicted in each individual plot as a black vertical line and its value under the x-axis (in italic). The asterisk after the participant number on top of each plot marks participants that were considered in the final analyses.

Figure 3. Depiction of the single significant cluster of ERP differences in the non-parametric cluster-based permutation test. (A) Grand average ERP which was additionally averaged over all channels of the significant cluster. Time points in the grey shaded area were part of the significant cluster. Shaded areas around each curve represent the 95% confidence interval based on the within-subject

standard deviation. (B) Topographic plots of the grand average ERP difference which was additionally averaged over all time points of the significant cluster in the depicted time intervals. Channels of the significant cluster are highlighted in white.

Figure 4. Depiction of the single significant cluster that resulted from POS values in the nonparametric cluster-based permutation tests. (A) Time-frequency plot of the sum of electrodes in which a certain time-frequency combination was part of a significant cluster. Shaded areas depict time-frequency combinations which may have been influenced by post-target activity. Sub-clusters that were chosen for closer inspection are outlined as colored boxes. (B) Topographical plots of a sub-cluster's average POS and ITC. Electrodes in which a sub-cluster's time-frequency combinations showed at least one significant POS are highlighted in white.

Figure 5. Depiction of *simultaneous* report proportions of each participant as a function of the phase state in either the alpha (A) or beta (B) frequency cluster center.

Figures

Figure 1

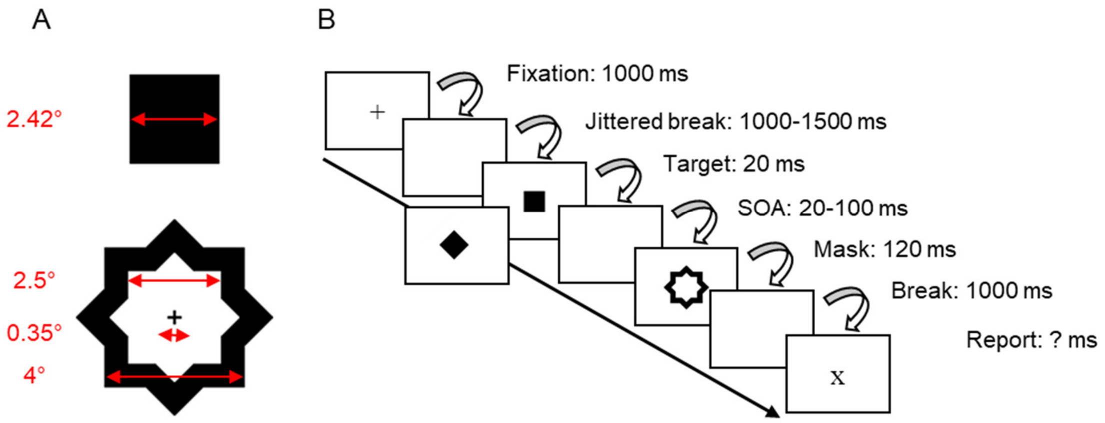
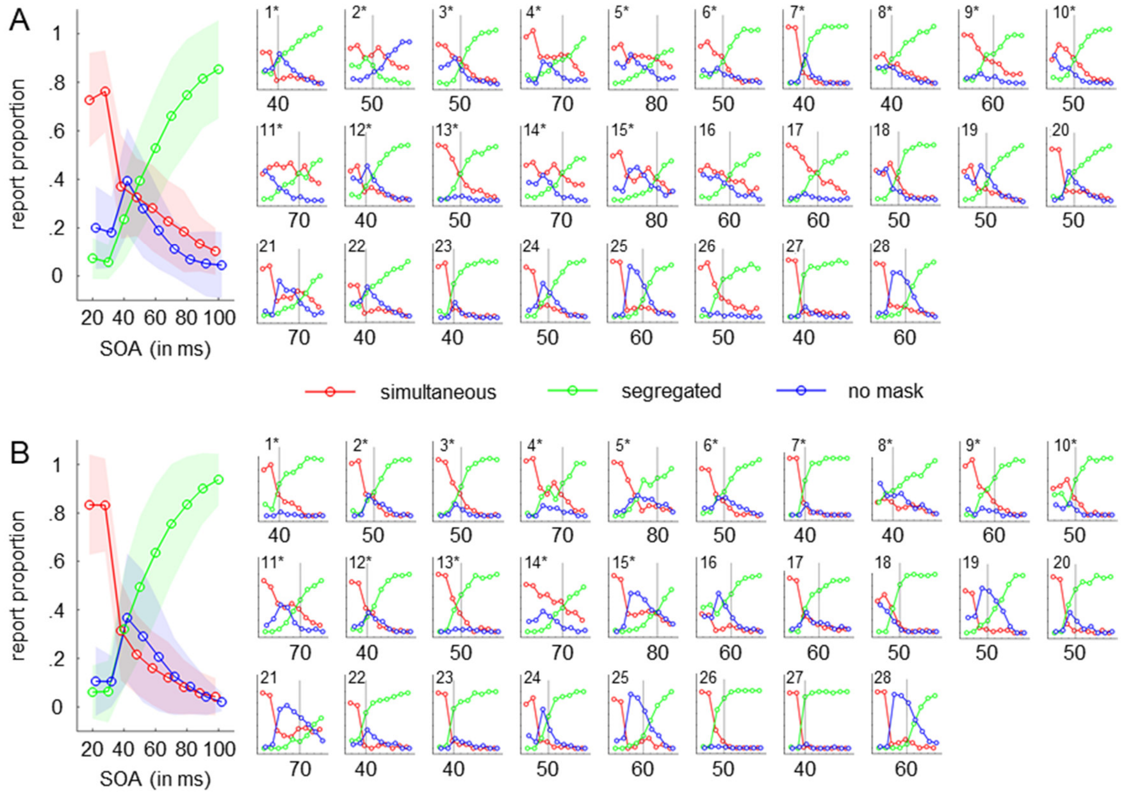


Figure 2


A
report proportion
1
.8
.6
.4
.2
0
20 40 60 80 100
SOA (in ms)
1* 40
2* 50
3* 50
4* 70
5* 80
6* 50
7* 40
8* 40
9* 60
10* 50
11* 70
12* 40
13* 50
14* 70
15* 80
16 60
17 60
18 50
19 50
20 50
21 70
22 40
23 40
24 50
25 60
26 50
27 40
28 60
simultaneous
segregated
no mask
B
report proportion
1
.8
.6
.4
.2
0
20 40 60 80 100
SOA (in ms)
1* 40
2* 50
3* 50
4* 70
5* 80
6* 50
7* 40
8* 40
9* 60
10* 50
11* 70
12* 40
13* 50
14* 70
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26 50
27 40
28 60

Figure 3

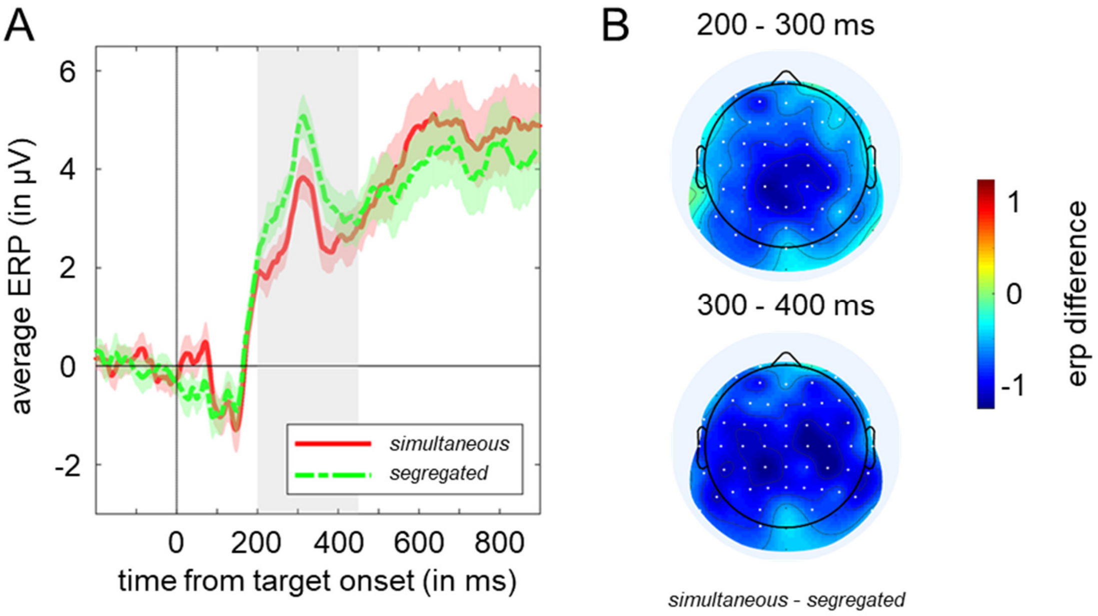

A
average ERP (in µV)
6
4
2
0
-2
0
200
400
600
800
time from target onset (in ms)
simultaneous
segregated
B
200 - 300 ms
300 - 400 ms
1
0
-1
erp difference
simultaneous - segregated

Figure 4

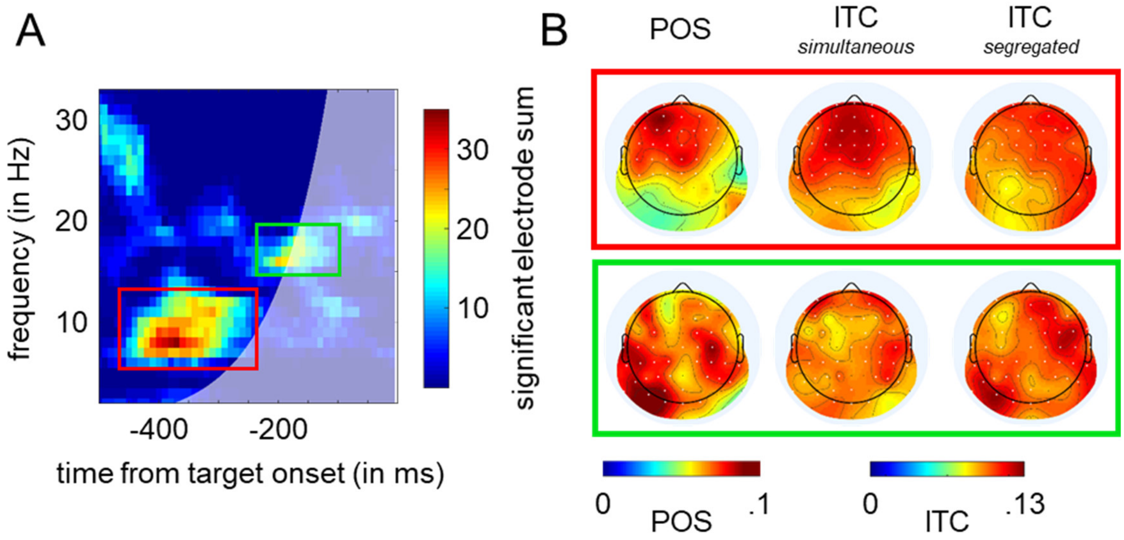
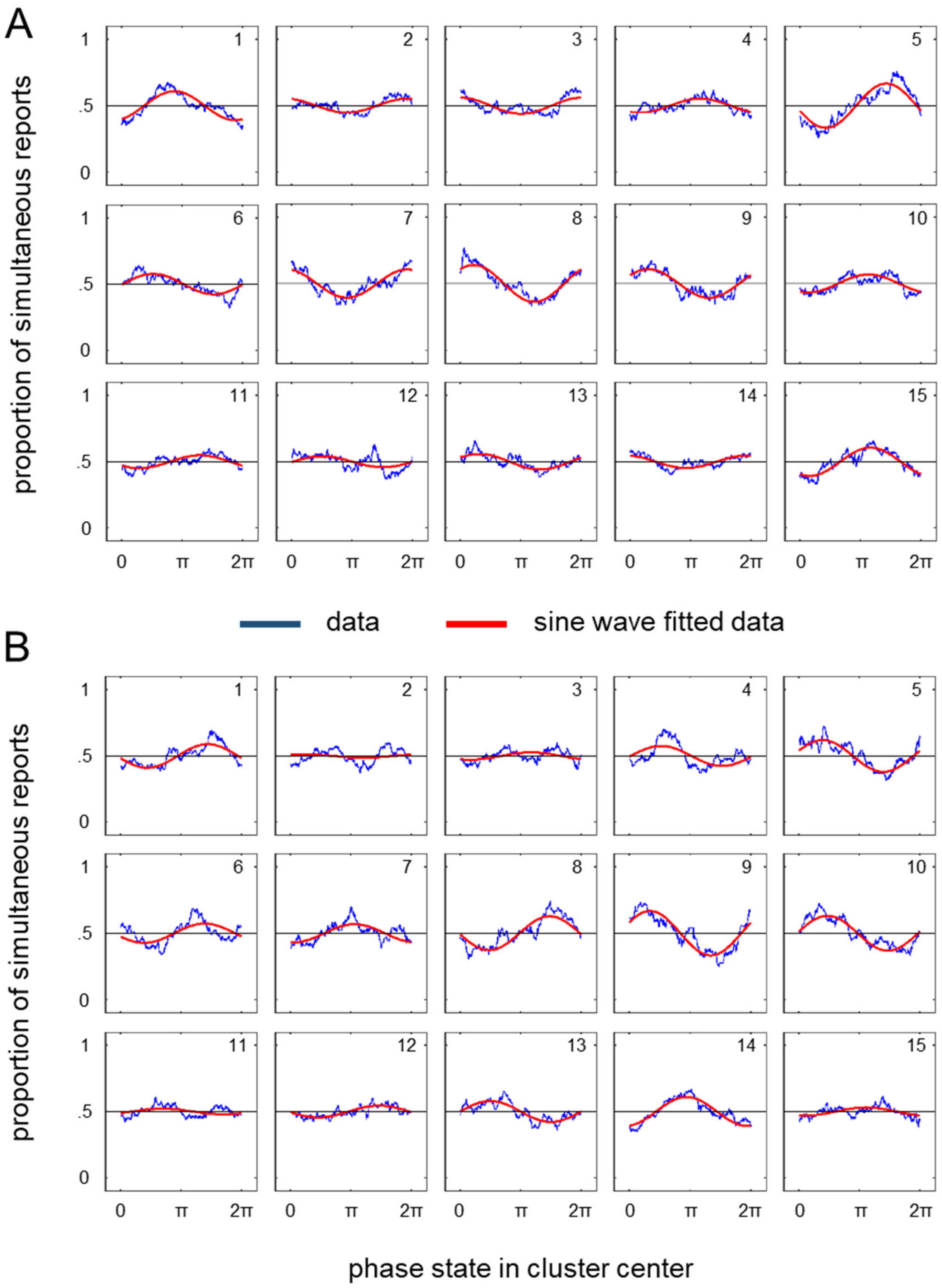

A
frequency (in Hz)
30
20
10
-400
-200
time from target onset (in ms)
30
20
10
significant electrode sum
B
POS
ITC
simultaneous
ITC
segregated
0
POS
.1
0
ITC
.13

Figure 5


A
proportion of simultaneous reports
1
.5
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0
π
2π
data
sine wave fitted data
B
proportion of simultaneous reports
phase state in cluster center

Supplementary information

for the manuscript

Neural correlates of temporal integration and segregation in metacontrast masking: a phenomenological study

by

Alexander T. A. Kraut, and Thorsten Albrecht

It contains the following sections:

1. Individual alpha frequency and temporal processing

Since it is still unclear whether all IAF measures reflect the same underlying processing characteristic of the visual system or not (Corcoran, Alday, Schlesewsky & Bornkessel-Schlesewsky, 2017) we decided to calculate three different IAF measures and compare their results: the peak alpha frequency (PAF; Corcoran et al., 2017), the center of gravity(CoG; Corcoran et al., 2017) and the IAF based on the channel reactivity-based method (CRB; Goljahani et al., 2012; Goljahani, Bisiacchi, & Sparacino, 2014). If not otherwise specified, all measures were calculated based on the default settings of the MATLAB functions that were forwarded by the respective authors. Three participants needed to be excluded from further analyses since at least one method to calculate the IAF failed.

In the end of the second session, the EEG was recorded with closed eyes for two continuous minutes allowing for the extraction of the IAF at rest. These resting phase data were bandpass filtered between 1 and 40 Hz (IIR Butterworth filter, 12 dB/octave) and separated into 30 non-overlapping epochs of four seconds. The first eight epochs were excluded from further analyses to be certain that participants were already at rest. Epochs with motoric, ocular or other artifacts were discarded from further analyses by visual inspection. On average 12.0% of artefactual trials needed to be excluded (*SD* = 20.1%). One participant needed to be excluded from resting state IAF analyses because of too many artefactual trials (> 50%). Occipito-partietal channels (O1, Oz, O2, PO7, PO3, POz, PO4, PO8) were considered for the calculation of each IAF measure. The signal of each channel and epoch was first detrended, then multiplied with a hamming window and eventually padded with zeros to increase the frequency resolution for each calculation to 0.25 Hz. The power spectral density of each channel and epoch was then calculated based on a fast Fourier transform. Frequency limits were set between 1 and 40 Hz. The same procedure was applied to extract the IAF from the time window before and after stimulus presentation of the task phase. This was especially relevant for the CRB since it cannot be calculated based on the resting phase data but needs a comparison between the power spectral densities of the time window before and after stimulus presentation of the task phase.

The relationship between the IAF and the behavioral data was assessed by spearman correlations between the IAF measures and the point of subjective equality (PSE) of both the *simultaneity* and *segregation* curves. We decided for the PSE since it reflects a participant's tendency to give the respective temporal report in longer or shorter SOA reflecting the temporal resolution of the visual system which should be related to the IAF (Samaha & Postle, 2015). It has to be noted that the PSE (first session) and IAF (second session) measures stem from data of two different sessions potentially weakening their correlation due to differences between sessions. However, since the IAF has been demonstrated to be a highly reliable measure (Grandy et al., 2013) we consider this influence to be small.

Spearman correlations between the different IAF measures as well as the PSE of the *simultaneity* and *segregation* curve are depicted in table S1. PAF and CoG showed very high and significant correlations with each other and correlated nearly perfectly with each other when both were calculated on either the resting or task phase data. In contrast, moderate significant correlations between the CRB and either the PAF or CoG resulted only for the task but not the resting phase data. No significant correlations could be found between any of the different IAF measures and the PSE of either the *simultaneity* or *segregation* curve. Moreover, the correlation between the PSE themselves did not reach significance.

Although it was demonstrated that the temporal resolution of our visual

Table S1

Spearman correlations and *p* values (in parentheses) for the relationship between different measures of the individual alpha frequency and the point of subjective equality (*n* = 24)

	PSE-Seg	PAF-Rest	CoG-Rest	PAF-Task	CoG-Task	CRB-Task
PSE-Sim	.40 (.06)	.16 (.46)	.09 (.67)	.14 (.52)	.12 (.59)	.21 (.34)
PSE-Seg		-.17 (.44)	-.24 (.28)	-.05 (.83)	-.06 (.78)	.08 (.73)
PAF-Rest			**.98 (.01)**	**.75 (.01)**	**.76 (.01)**	.35 (.11)
CoG-Rest				**.79 (.01)**	**.80 (.01)**	.39 (.07)
PAF-Task					**.99 (.01)**	**.57 (.01)**
CoG-Task						**.59 (.01)**

PSE-Sim = Point of subjective equality of the *simultaneity* curve

PSE-Seg = Point of subjective equality of the *segregation* curve

PAF-Rest = Peak alpha frequency calculated from resting phase data

CoG-Rest = Center of Gravity calculated from resting phase data

PAF-Task = Peak alpha frequency calculated for the pre-stimulus time window

CoG-Task = Center of Gravity calculated for the pre-stimulus time window

CRB-Task = Individual alpha frequency calculated by the channel-based reactivity method for the pre-stimulus and post-stimulus time window system is individually variable and correlated to the individual alpha frequency (Samaha & Postle, 2015), we did not find any relationship between the individual alpha frequency and our behavioral data. This missing relationship may be due to a difference in the complexity of the stimuli that were used in our and previous studies that used for example the two-flash task. Whereas lower levels of the visual hierarchy may be sufficient for temporally processing flashes, higher levels may be required for the temporal processing of the target-mask sequence. Against this background, the relevance of the individual alpha frequency in temporal processing would be limited to early stages of visual processing.

2. Supplementary analyses

Table S2

z and *p* values (in parentheses) for the results of the linear and quadratic trend analyses using a logistic regression to predict report proportions as a function of the SOA (*n* = 28). Slopes were allowed to vary randomly for each participant.

	session 1		session 2	
	linear	quadratic	linear	quadratic
simultaneous	-11.45 (.00)	3.00 (.00)	-10.39 (.00)	3.84 (.00)
segregated	15.74 (.00)	-4.51 (.00)	16.31 (.00)	-3.47 (.00)
only mask	-8.42 (.00)	-6.21 (.00)	-6.62 (.00)	-9.03 (.00)

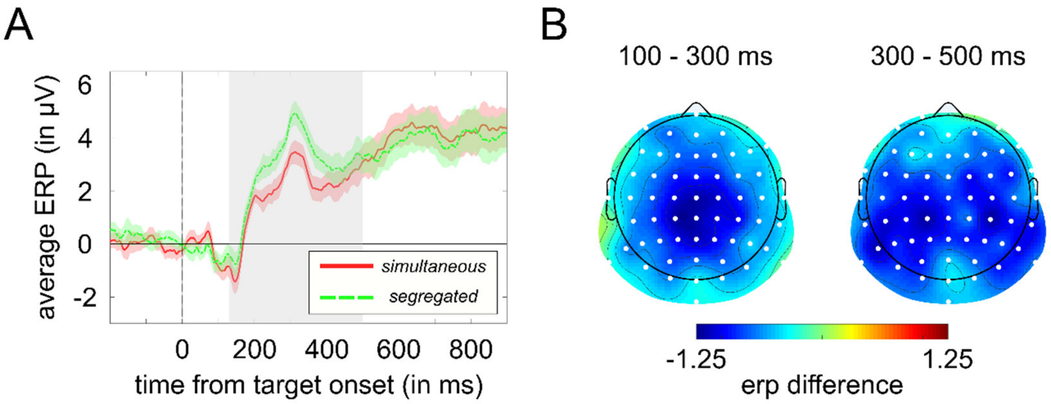


Figure S1. Depiction of the single significant cluster (*p* = .011) of ERP differences in the nonparametric cluster-based permutation test. ERPs were calculated with regard to the mask onset. (A) Grand average ERP which was additionally averaged over all channels of the significant cluster. Time points in the grey shaded area were part of the significant cluster. Shaded areas around each curve represent the 95% confidence interval based on the within-subject standard deviation. (B) Topographic plots of the grand average ERP difference which was additionally averaged over all time points of the significant cluster in the depicted time intervals. Channels of the significant cluster are highlighted in white.

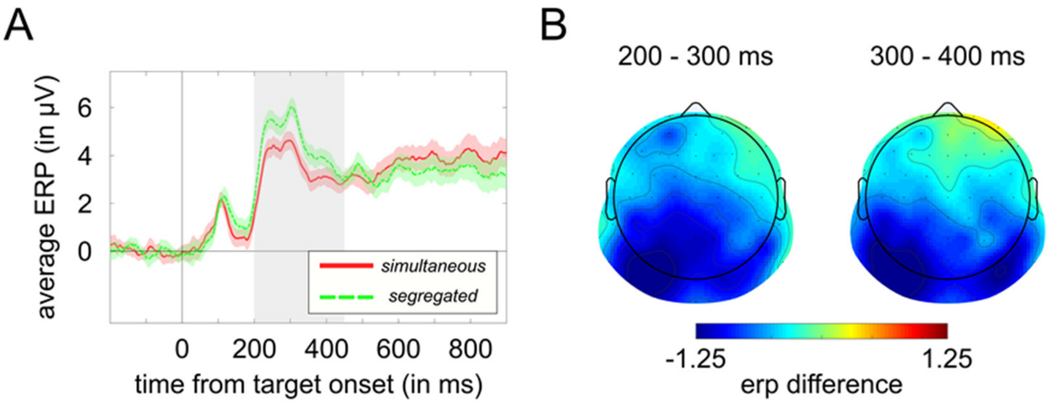


Figure S2. Depiction of ERP differences resulting from incorporating all participants with at least 20 trials in each report category into the analysis (*n* = 24). No significant clusters emerged from the non-parametric cluster-based permutation test. Thus, the plots that are depicted here are based on the largest non-significant cluster (*p* = .055). (A) Grand average ERP which was additionally averaged over all channels of the largest non-significant cluster. Shaded areas around each curve represent the 95% confidence interval based on the within-subject standard deviation. (B) Topographic plots of the grand average ERP difference which was additionally averaged over all time points of the depicted time intervals.

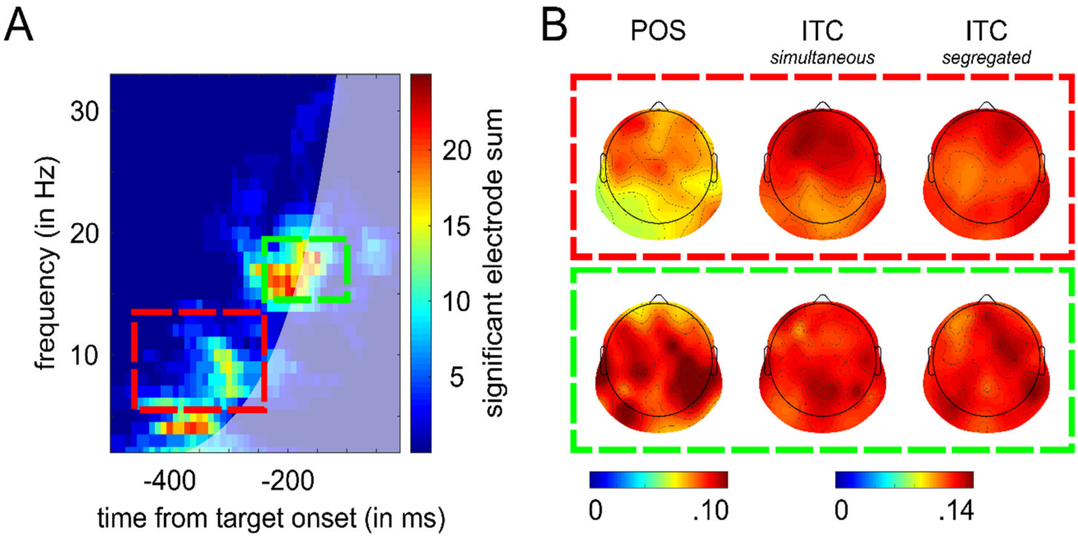


Figure S3. Depiction of POS and ITC values that resulted from incorporating all participants with at least 20 trials in each report category into the analysis ($n = 24$). No significant cluster emerged from the non-parametric cluster-based permutation test. Thus, the plots that are depicted here are based on the largest non-significant cluster ($p = .206$). (A) Time-frequency plot of the sum of electrodes in which a certain time-frequency combination was part of the largest non-significant cluster. Shaded areas depict time-frequency combinations which may have been influenced by post-target activity. Sub-clusters that were chosen for closer inspection are outlined as colored boxes and were adopted from the main analysis. (B) Topographical plots of a sub-cluster's average POS and ITC.

3. Supplementary references

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Appendix II - manuscript for study 2

Kraut, A. T., Sandberg, K., & Albrecht, T. (2022). *Neural sources of temporal integration and segregation in metacontrast masking: a MEG study* [Unpublished manuscript]. Department of Experimental Psychology, University Göttingen.

Manuscript title

Neural sources of temporal integration and segregation in metacontrast masking: a MEG study

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Abstract

Temporal integration and segregation mechanisms play an increasingly important role in masking theories. Some theories even propose that there is no masking mechanism at all but that masking results in the absence of temporal processing. Accordingly, temporal and masking phenomena should share the same neural sources and processes. Thus, the aim of this study was to determine the neural sources of temporal integration and segregation in a metacontrast masking paradigm and compare them to those of masking. Participants reported on each trial whether they perceived the target-mask sequence temporally integrated or segregated while their MEG was concurrently recorded. A comparison of both report categories resulted in pre-stimulus phase differences in the theta, alpha and beta frequency band. Whereas phase differences in the theta and alpha frequency band were localized in occipito-temporal brain areas, phase differences in the beta frequency band were localized in fronto-temporal brain areas. Temporal areas of the right hemisphere depicted both pre-stimulus phase differences in the theta and beta frequency band as well as post-stimulus ERF differences. Our results replicate the neural correlates of temporal integration and segregation that we have previously demonstrated in a metacontrast masking paradigm. Our source localization expands on these results and implicates lower neural frequencies to be associated with bottom-up temporal processing and higher frequencies to be associated with a top-down influence on temporal processing. Since we are able to demonstrate an overlap between the neural sources of temporal and masking mechanisms we would recommend a concurrent investigation of both temporal and masking mechanisms in future studies.

1. Introduction

Complex systems that are comprised of multiple individual units are often organized by some means of synchronization and rhythmicity. Take for example musicians in an orchestra whose individual performances are synchronized by the rhythm of the music and the steadily repeating times that ensure the functionality of the orchestra as a system at large. By far the most complex system we know to date is the human brain, and a growing body of evidence suggests that neural rhythms or oscillations are a key component of information processing and cognitive and perceptual functioning (Başar, Başar-Eroğlu, Karakaş, & Schürmann, 1999, 2000, 2001; Jensen, Spaak, & Zumer, 2014). Recent research suggests an important role of neural oscillations in basic (visual) perception and the temporal organization of the continuous flow of information received by our senses (e.g. VanRullen & Koch, 2003; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Jensen, Gips, Bergmann, & Bonnefond, 2014; VanRullen, 2016a).

When two successive stimuli are presented in close temporal proximity, they are often misperceived as being simultaneously presented. This has been demonstrated for the visual (e.g., Exner, 1875; Di Lollo, Hogben, & Dixon, 1994), the auditory (e.g. Fujioka, Trainer, Large & Ross, 2012; Arnal, Doelling & Poeppel, 2015) and the somatosensory (e.g, Baumgarten, Schnitzler, & Lange, 2015) domain. These findings indicate that our neural system creates a non-perfect temporal representation of our external environment which may result from partitioning the continuous flow of external stimulation into a succession of distinct and discrete chunks of information, so called “perceptual moments” (Stroud, 1956; Block, 2014). Such a discrete perception may originate from “perceptual cycles" (VanRullen, 2016a) in our neural processing (VanRullen & Koch, 2003). Especially neural signals in the lower frequency range of the theta (3 to 6 Hz; Hanslmayr et al., 2013) and alpha frequency band (7 to 14 Hz; Lindsley, 1952; Jensen et al., 2014) are proposed to orchestrate neural processing by rhythmically moderating the excitability of the underlying neural substrate (VanRullen & Koch, 2003; VanRullen, 2016a). Whereas the neural substrate is maximally inhibited when the oscillatory cycle reaches its maximum, it is least inhibited when the oscillatory cycle reaches its minimum.

The rhythmic alternation between increased and decreased excitability has been proposed to form temporal integration windows around the time points of maximum excitability (Varela, Torro, John & Schwartz, 1981). Within this theoretical framework, successively presented stimuli are perceived as simultaneous or sequential depending on whether they fall in the same or different temporal integration windows (Samaha & Postle, 2015; Ronconi, Oosterhof, Bonmassar, & Melcher, 2017; Ronconi & Melcher, 2017). The ability to adjust the width of the temporal integration window depending on task requirements would then allow the visual system to dynamically balance integration and segregation (Wutz, Melcher, & Samaha, 2018).

To avoid the strong assumption of discrete time windows of integration, other approaches link the alternating neural excitability to the accuracy of temporal representations (Milton & Pleydell-Pearce, 2016) or to the latency of stimuli exceeding a perceptual threshold (VanRullen, 2016a). Specifically, Milton and Pleydell-Pearce (2016) suggest that stimuli and the time between them are more accurately represented, when they are processed in phases of high neural excitability, thus leading to a more accurate (sequential) perception. In contrast, VanRullen (2016a) suggests that stimuli that are processed in phases of low excitability reach the perceptual threshold later than stimuli that are processed in phases of high excitability. This mechanism would then result in differences between the actual and perceived temporal delay between the presentation of two stimuli. The claim of phase-dependent differences in perceptual thresholds has been backed up by several studies using either backward masking (Mathewson et al., 2009) or near-threshold stimuli (Busch, VanRullen, & Dubois, 2009).

In metacontrast masking, a specific form of backward masking, the visibility of a target stimulus is reduced through the subsequent presentation of a masking stimulus to the extreme of not perceiving the target at all. This masking effect has been demonstrated to be weaker when the target is presented in the minimum of the alpha cycle and stronger when the target is presented in the maximum of the alpha cycle especially with concurrently high alpha power (Mathewson et al., 2009). The authors conclude that the excitability of the neural substrate changes within one cycle of the alpha frequency terming it a “pulsed inhibition” (Mathewson, Lleras, Beck, Fabiani, Ro & Gratton, 2011). Similarly, the detection performance of visual stimuli presented at or near threshold is modulated by power and phase of alpha activity (Busch et al., 2009; Busch & VanRullen, 2010) and are in line with the idea that there are time windows of increased or decreased neural excitability.

Since both temporal and masking phenomena may result from the oscillatory character of our neural processing, they may share overlapping neural mechanisms. In addition, there is growing evidence that temporal integration and segregation are closely related to visual masking (Reeves, 1982; Francis & Cho, 2008; Albrecht & Mattler, 2016; Koster, Mattler, & Albrecht, 2020; Kraut &

Albrecht, 2022). According to Reeves' (1982) dual process theory, temporal integration and segregation constitute two independent processes that are key components of metacontrast masking. Whereas the temporal integration process is strongest in short SOA and shows a declining strength with increasing SOA, the temporal segregation process is strongest in long SOA and shows a declining strength with decreasing SOA. Due to their independence both processes may concurrently fail from which masking should result. Since both temporal processes are equally weak in medium SOA, masking should also be most likely in medium SOA. Since no third masking process is implied in this theory, neural correlates of temporal integration and segregation should directly relate to the neural correlates that have been demonstrated for masking.

However, research on temporal and masking mechanisms in vision has only rarely been combined. This is especially remarkable since on the one hand, most paradigms that investigate temporal integration and segregation mechanisms may suffer from a masking confound (Akyürek & Wijnja, 2019; Kraut & Albrecht, 2022) and on the other hand, temporal integration and segregation play an important role in models to explain the masking phenomenon (Reeves, 1982). As a first step towards a unification of temporal and masking mechanisms, we previously generalized the neural correlates of temporal integration and segregation to metacontrast masking using a phenomenal approach combined with EEG measures (Kraut & Albrecht, 2022). In each trial, participants reported their phenomenal perception of the target-mask sequence as either temporally integrated, temporally segregated or masked. We then compared trials with a temporally integrated to trials with a temporally segregated report of the target-mask sequence and investigated pre-stimulus power and phase differences and post-stimulus

ERP differences. This comparison showed phase differences in the alpha frequency band (7 to 14 Hz) between 450 and 250 ms before target onset which supports the idea that the excitability of the neural substrate also affects temporal processing in the metacontrast masking paradigm. We also found phase differences in the lower beta frequency band (15-20 Hz) between 225 and 125 ms before target onset which have not been reported for temporal processing in vision before. Additionally, we found more negative ERP amplitudes between 200 and 400 ms after target presentation for temporally integrated reports over centro-parietal electrodes that might reflect a contour integration process (contour integration negativity, CIN; Pitts & Martinez, 2014). Our centro-parietal localization of the CIN deviates from its occipito-temporal localization that was reported in the original literature (Pitts & Martinez, 2014) in which single low-level stimulus displays with and without contours were compared against each other. Our localization of the CIN in more frontal electrodes may be due to our more complex stimulus presentation in which not one but two stimuli needed to be neurally represented and later on temporally integrated for differences in contour processing to arise.

An ERP component that occurs in metacontrast masking in a similar time range as the CIN is the visual awareness negativity (VAN; Railo, Koivisto, & Revonsuo, 2011). The VAN results from a comparison of masked and unmasked trials and reflects a more negative amplitude for unmasked trials in the time range of the N1 and N2 ERP component in occipito-temporal electrodes. Both the CIN and VAN have been demonstrated to be separable from each other (Pitts & Martinez, 2014) which fits our finding that both of them show a different topography in metacontrast masking. The VAN is usually followed by a late positivity (LP; Del

Cul, Baillet & Dehaene, 2007; van Aalderen-Smeets, Oostenveld & Schwarzbach, 2006) showing a more positive amplitude in centro-parietal electrodes for unmasked trials in the time range of the P3 component. While the LP has been linked to post-perceptual processes and processes in the global workspace (Del Cul et al., 2007; Förster, Koivisto, & Revonsuo, 2020), the VAN has been linked to processes in the ventral stream and the emergence of conscious visual percepts (Railo et al., 2011). Findings from masking studies using fMRI also locate masking effects in the ventral stream and associate them with a decoupling between the occipital and temporal cortices (Haynes, Driver, & Rees, 2005; Imamoglu, Heinzle, Imfeld, & Haynes, 2014). In addition, there is evidence that not only activity in occipital and temporal but also activity in parietal, frontal and even subcortical (Putamen, Insula) brain areas correlates with masking effects (Haynes et al., 2005; Imamoglu et al., 2014; Albrecht, Krüger & Mattler, 2013).

To our knowledge, there are yet no studies that investigate the neural sources of phenomenal reports neither in in the pre-stimulus nor in the post-stimulus time window. Therefore, the current study is largely explorative. The aims of the current study are two-fold. First, we want to replicate and expand on our previous findings of pre-stimulus phase differences in the alpha and beta frequency bands in metacontrast masking (Kraut & Albrecht, 2022). Second, we aim to identify the neural sources of temporal integration and segregation both before and after stimulus presentation. These results will add to the sparse evidence on the neural sources of temporal integration and segregation (e.g. Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016) and will allow us to compare the neural sources of our temporal effects with that of masking effects reported in the literature. If masking effects are dependent on temporal processes (Reeves, 1982), we would expect to find similar neural sources for both temporal and masking effects.

To this end, we conducted a MEG study using a comparable but enhanced metacontrast masking paradigm as reported previously (Kraut & Albrecht, 2022). The MEG is a complementary measurement device to the EEG and well suited for source localization since it provides a sufficient number of channels and a signal that is both reference-free as well as less distorted than that of the EEG. Participants reported in each trial their phenomenal (temporal) perception of the target-mask sequence while their neural activity was measured. We then compared the pre-stimulus power and phase states and the post-stimulus event-related fields (ERF) between trials with a temporally integrated and segregated report. For the analyses, we projected the neural effects into source space prior to conducting inference statistics.

2. Methods

2.1 Participants

27 students from the Aarhus University participated in this study for financial compensation. Prior to the experiment all participants gave their informed consent. Three participants needed to be excluded from the study since they did not fulfill the initial inclusion criteria of having no neural disease (n = 1), having no unremovable metal on their body (n = 1) or having no uncorrected visual impairment (n = 1). Six further participants needed to be excluded from all MEG analyses since they had too less trials in at least one of the temporal report categories. Thus, 18 participants (ten female) between 18 and 27 years old (*M* = 22.6, *SD* = 2.4) were included in the MEG analyses. All participants were right handed

and reported to have normal or corrected to normal vision.

2.2 Stimuli

The experiment was programmed in *MATLAB* (MATLAB 9.4; MathWorks) using the *Psychophysics Toolbox* (Brainard & Vision, 1997; Pelli & Vision, 1997; Kleiner, Brainard, & Pelli, 2007) and was presented on a screen using a *PROPixx* projector (*VPixx Technologies Inc.*) with a refresh rate of 480 Hz. All stimuli were presented in black on a white background in the center of the screen. Target stimuli were filled squares and diamonds. The masking stimulus was an eight-pointed star whose interior was cut out so that both targets would fit inside. A fixation cross was continuously presented to help participants to fixate the center of the screen. Figure 1a depicts all stimuli and their sizes.

**** Insert figure 1 here ****

2.3 Task

After each presentation of the target-mask sequence (figure 1b) participants had to report the perceived temporal succession of target and mask in a three-choice task that we adopted from one of our previous studies (Kraut & Albrecht, 2022). A *simultaneous* perception should be reported if some visual feature of the target could be perceived inside of the white space of the mask. A *segregated* perception should be reported if some visual feature of the target could be perceived temporally before the mask and the white space of the mask stayed empty. A *mask only* perception should be reported if absolutely no visual feature of the target could be perceived. It was emphasized that it is sufficient to perceive only some visual feature of the target (a blackish shadow, only the edges or the contour of the target, etc.) to either report a *simultaneous* or *segregated* perception since the presentation would usually be too fast to have a clear perception of the target. In cases in which the target could be both perceived inside of the white space of the mask (*simultaneous*) and temporally before the mask (*segregated*) participants were instructed to report the most dominant perception. Participants indicated their temporal reports using three buttons on a button box. The assignment of temporal reports to buttons was counterbalanced over participants.

2.4 Procedure

The experiment consisted of two sessions that took place on two successive days. The trial sequence was identical for each session. Each trial started with the presentation of the fixation cross for 2000 to 2500 ms. Afterwards, the target was presented for 21 ms (10 frames) followed by the mask for 31 ms (15 frames). Target and mask were never presented at the same time but were always temporally separated from each other by a variable SOA. The SOA varied between 21 to 104 ms (10 to 50 frames) in evenly spaced steps of 21 ms (10 frames). The mask presentation was followed by a blank screen for 1000 ms, in which only the fixation cross was presented. At the end of each trial, the fixation cross became thicker, thereby indicating that the temporal perception of the target-mask sequence can now be reported. Participants had no time limit for their response but were asked to evaluate their perception as spontaneously as possible. Each session comprised 720 trials that were organized in 20 blocks with 36 trials each. Both target shape as well as SOA varied pseudo-randomly within each block.

Each recording session lasted around 60 minutes.

The aim of the first session was to make participants feel comfortable about the task so that they developed a reliable set of criteria for each report category that they could then apply in the second session. The first four blocks of the second session were used to identify the SOA for which *simultaneous* and *segregated* reports occurred equally often. This *primary SOA* was determined separately for each participant. It was presented in half of all trials in the remaining sixteen blocks of the second session to get as many trials with constant physical stimulation but varying temporal reports as possible (288/576 trials). All other SOA were presented with equal proportions in the other half of all trials. It was possible that one of these SOA coincided with a participant's *primary SOA* so that the *primary SOA* was presented more often (320/576).

Temporal report categories were thoroughly explained to each participant in the beginning of each session. To monitor the understanding of these categories, participants were asked to explain each report category and their respective perceptual criteria in their own words both in the beginning and end of each session as well as after the first block of the first session and were corrected if necessary.

2.5 Behavioral data

The *primary SOA* was determined for each participant based on the first four blocks of the second session. Based on these trials, the proportions of trials with *simultaneous* and *segregated* reports were averaged separately for each SOA and temporal report category and afterwards fitted by a cumulative normal function using the Palamedes toolbox (Prins & Kingdom, 2009) for MATLAB. All curve parameters (point of subjective equality, slope, guess rate and lapse rate) were left free to vary whereby the guess and lapse rate were restricted to values between 0 and .2. As a function of SOA, the curves of all participants showed a negative slope for *simultaneous* reports and a positive slope for *segregated* reports. Consequently, both curves intersected for each participant and the SOA closest to this intersection was used as *primary SOA* in the remaining blocks of the second session. In cases in which the intersection was located outside of the SOA range used in this study, a SOA that was still in the SOA range but was closest to the intersection was used as *primary SOA* (this happened only once).

2.6 Magnetoencephalographic data

2.6.1 Data collection and preprocessing prior to source localization

MEG data were recorded in an electromagnetically shielded room (*Vacuum Schmeltzer GmbH*) using an *Elekta Neuromag TRIUX MEG* setup with 102 magnetometers and 204 planar gradiometers (*Elekta Neuromag Oy*). Additionally, using a motion tracking setup (*3Space Fastrak*; *Polhemus*, Colchester, Vermont) we recorded between 636 and 1353 (*M* = 924.1, *SD* = 232.1) evenly distributed spatial positions on the scalp of each participant to create individual head shape models. To control for eye movements, three electrodes were placed at the outer canthi of both eyes and under the right eye. To continuously track participants' head position and head movement, head position indicator coils were placed behind each ear and the left and right hairline edges of the forehead. Data were recorded with a sampling frequency of 2000 Hz, a high-pass filter of .1 Hz and a low-pass filter of 330 Hz (IIR Butterworth filter, 6th order). Participants were seated upright in the MEG.

Signal space separation (Taulu & Simola, 2006) was conducted using the MaxFilter algorithm (*Elekta Oy*, Helsinki, Finland) with default settings to remove signals from sources outside of the brain. Afterwards MEG data were preprocessed and analyzed using the FieldTrip toolbox (Oostenveld, Fries, Maris & Schoffelen, 2011) for MATLAB. MEG data were downsampled to 500 Hz, high-pass filtered at .1 Hz (IIR Butterworth filter, 5th order), low-pass filtered at 100 Hz (IIR Butterworth filter, 4th order) and afterwards segmented into epochs from 1000 ms before target onset to 1000 ms after target onset. Epochs with large motor artefacts were discarded by visual inspection before an independent component analysis (Jung et al., 2000) was used to correct for ocular artefacts. Subsequently, the data were once again visually inspected for remaining artefacts. On average 9.5% epochs (*SD* = 9.6%) needed to be excluded. Only data from magnetometers were considered for the following analyses since (1) combining the information from both gradiometers and magnetometers is non-trivial and (2) both sensor types are argued to contain the same information (after signal space separation; Garcés, López-Sanz, Maestú, & Pereda, 2017).

Only trials with the *primary SOA* were included in the MEG analyses thereby keeping physical stimulation for each participant stable. Nonetheless, the *primary SOA* varied between participants. Participants were included in the MEG analyses if they reported a *simultaneous* or *segregated* perception each in at least 50 trials that used their *primary SOA*. Six participants needed to be excluded since they did not meet this criterion. For the remaining 18 participants the number of trials in each report category was equalized by randomly drawing as many trials from the report category with more trials as there were trials in the report category with less trials. Eventually, between 53 and 112 trials for each temporal report category (*M* = 76.0, *SD* = 16.0) were forwarded to the magnetoencephalographic analyses for each participant. The number of trials with an o*nly mask* report ranged between 0 and 187 trials (*M* = 58.0, *SD* = 53.1) and were not included in any exploratory MEG analysis since only seven participants had enough trials for both a *simultaneous*, *segregated* and *only mask* report.

2.6.2 Source localization

We estimated each participant's structural MRI volume by affinely transforming a template MRI volume from the Montreal Neurological Institute (MNI; Cocosco, Kollokian, Kwan, & Evans, 1997) to each participant's head shape model. MNI-aligned grids were created for each participant by warping the individual MRI to the template MRI and applying the inverse of this transformation matrix to an MNI-aligned grid with 1080 grid points and 15 mm spacing. To get a reliable spatial filter for each source analysis, a common spatial filter was calculated based on all trials and then applied to each trial to project its data into source space.

2.6.3 Event-related fields

For the analyses of event-related fields (ERF) the preprocessed data were high-cut filtered at 30 Hz (IIR Butterworth filter, 4th order) and then projected into source space using the linear constrained minimum variance beamformer algorithm (Van Veen, Van Drongelen, Yuchtman, & Suzuki, 1997). Within the source space, a relative baseline correction was performed separately for each trial based on the 200 ms prior to target presentation. Average ERF differences between report categories were calculated and tested for significance.

2.6.4 Time frequency decomposition

Before projecting the neural signals into source space, wavelet analyses were performed for each participant, all frequencies between 3 and 29 Hz in steps of 2 Hz and all time points between 500 and 0 ms before target onset in steps of 25 ms. The number of cycles was increased for higher frequencies to counter differences in frequency precision for higher compared to lower frequencies (Cohen, 2014). Hence, we started with 1 cycle for the 3 Hz frequency and increased the number of cycles linearly up to 14 cycles for the 29 Hz frequency. Accordingly, it is inherent to wavelet analyses to estimate the complex values for a single time point by also considering data in neighboring time points. As a result, the estimated complex values for time points before target presentation that are however close to target presentation may already be confounded by activity after target presentation. We therefore only interpret significant effects before target presentation that cannot have resulted from activity after target presentation. Eventually, the complex values of the wavelet analysis were projected into source space using the partial canonical correlation analysis algorithm (Rao, 1969).

After projecting the neural signal into source space, phase and power data were calculated. Power data were baseline-corrected using the condition-average of the whole 500 ms time window before target presentation as a relative baseline (see e.g. Cohen, 2014). Averaged power differences between report categories were calculated and tested for significance. To evaluate phase differences between report categories, the phase opposition sum (POS) was calculated (VanRullen, 2016b). The POS is calculated as the sum of inter-trial coherences (ITC) in each report category and is then corrected by the overall inter-trial coherence irrespective of report category:

$$\mathrm{POS} = \mathrm{ITC}_{Simultaneous} + \mathrm{ITC}_{Segregated} - 2 * \mathrm{ITC}_{Simultaneous\,\&\,Segregated}$$

Based on this formula, a high POS results from (1) a high ITC in each report category and (2) a phase shift in between of them. Since the ITC ranges between 0 and 1, the POS practically ranges between 0 and 2.

2.6.5 Statistical analyses

ERF differences, power differences and POS were analyzed using a threshold-free cluster-enhancement (TFCE) procedure (Smith & Nichols, 2009) in combination with nonparametric permutation tests (Maris & Oostenveld, 2007). TFCE procedures omit the necessity of defining an arbitrary significance threshold to create clusters of significant activity by weighing the statistical significance of each value with the number of neighboring values that depict the same effect direction and are also statistically significant (Smith & Nichols, 2009). Hence, a single significant value must not be mistaken for an isolated effect but needs to be interpreted as reflecting the peak effect size of a cluster of neighboring values that show the same effect but to a smaller degree. For the power and POS analysis, all voxels, frequencies and time points before target presentation were inserted into the TFCE procedure. For the ERF analysis all voxels and time points after target presentation were inserted into the TFCE analysis.

In order to apply the TFCE procedure, each element in the voxel-time(-frequency) maps of the empirical data was z standardized using the mean and standard deviation of its respective permutation distribution. To generate permutation distributions a surrogate dataset was calculated as the median of 1000 permutations for which trials were randomly assigned to each report category. Next, the permutation distribution was generated by fully permuting empirical and surrogate datasets across participants (2^{18} = 262 144 permutations). To reduce computation time only a subset of 10 000 permutations were calculated. The resulting voxel-time(-frequency) maps of z values for the empirical dataset were then entered into the TFCE procedure resulting in voxel-time(-frequency) maps of TFCE values.

To determine the significance of an empirical TFCE value, it was compared to a distribution of permuted TFCE values. To generate this distribution, all voxel-time(-frequency) maps of the previously calculated 10 000 datasets of the permutation distribution were also z standardized and entered into the TFCE procedure. The largest TFCE value was then extracted from each voxel-time(-frequency) map resulting in a distribution of 10 000 largest TFCE values. The upper 5th percentile of this distribution was used as significance threshold for the empirical TFCE values.

3. Results

3.1 Behavioral data

Figure 2 depicts the proportions of each report category for averaged data (A) and individual data (B) of the last sixteen blocks of the second session. Over the course of the SOA, the average proportions of *simultaneous* reports decreased and that of *segregated* reports increased. Both courses intersected and showed the same average report proportion in the 50 ms SOA. The average proportion of *only mask* reports showed an inverse U-shaped course over the SOA and peaked at the 50 ms SOA. Therefore, the intersection of the temporally integrated and segregated courses as well as the peak masking proportion coincide in the same SOA. With the exception of the linear trend of *only mask* reports, all linear and quadratic trends were significant for each report category (see table 1 in the supplements). Though all individual data courses show the same data pattern participants differ with respect to the overall amount of masking (*M* = .13, *SD* = .11, range = .00-.38) and their primary SOA (*M* = 57.46 ms, *SD* = 18.74 ms, range = 31.25-104.17 ms). Individual data patterns remained stable over the course of the second session shown by a high retest reliability of the *primary SOA* that was determined both for the first four and last sixteen blocks of the second session (*r*(22) = .88, *p* < .001).

**** Insert figure 2 here ****

3.2 Event-related fields after target presentation

Significant ERF differences resulted for three clusters of voxel-time combinations all showing a larger ERF for trials with a *simultaneous* compared to a *segregated* report (figure 3). The first cluster of significant ERF differences incorporated the time point 385 ms after target onset and was located in temporal areas of the right hemisphere. The latter two clusters incorporated the time points from 505 to 515 ms and 635 to 645 ms and were both localized in frontal areas of the left hemisphere.

**** Insert figure 3 here ****

3.3 Power and pos effects before target presentation

Significant power differences resulted for the 5 Hz frequency 375 ms before target presentation depicting lower power values for *simultaneous* compared to *temporally segregated* reports (figure 4). This effect was localized in a single voxel in temporal regions of the left hemisphere. All significant power differences were restricted to this single voxel-time-frequency combination.

**** Insert figure 4 here ****

Significant POS values resulted for a large amount of voxel-time-frequency combinations of which we further investigated four clusters of time-frequency combinations for which especially many voxels became significant (>150 voxels, figure 5). We will differentiate these clusters in the following according to their onset (early vs. late) and frequency band (alpha/theta vs. beta). The beta clusters incorporated frequencies from 13 to 19 Hz and time points from 500 to 400 ms for the early and 400 to 250 ms for the late beta cluster. In source space the early beta cluster showed a localization in frontal regions of the left hemisphere and cento-temporal regions of the right hemisphere. This then changed for the late beta cluster to a localization in occipito-temporal regions of the right hemisphere. Hence, over time, the source localization of phase differences in the beta clusters shifted from more fronto-temporal to more occipito-temporal regions. The early alpha cluster incorporated frequencies from 7 to 11 Hz and time points from 500 to 400 ms before target onset. In source space this cluster is especially located in occipito-parietal regions centered on the midline of the brain. The late theta cluster incorporated frequencies from 5 to 7 Hz and time points from 300 to 150 ms before target onset. In source space this cluster spanned occipital to frontal regions but was especially localized in cento-temporal regions of the right hemisphere.

**** Insert figure 5 here ****

4. Discussion

To determine the neural correlates and sources of temporal integration and segregation, we conducted a metacontrast masking experiment asking participants to report on their phenomenal temporal perception of the target-mask sequence. Participants' neural activity was concurrently recorded via MEG, projected into source space and contrasted between reports of temporally integrated and segregated percepts. In the pre-stimulus time window, we found phase differences in the theta, alpha and beta frequency band. Phase differences in the theta and alpha frequency band were mainly localized in occipito-temporal brain areas. Phase differences in the beta frequency band were mainly localized in fronto-temporal brain areas. In addition, temporally integrated reports showed a reduced power in temporal brain areas of the left hemisphere. In the post-stimulus time window, we found larger ERF amplitudes for temporally integrated reports for both temporal brain areas in the right hemisphere (385 ms) and frontal brain areas in the left hemisphere (510 ms, 640 ms). Overall, the anterior temporal lobe was implicated in most of our results and showed ERF, power and phase differences.

4.1 Behavioral results

Proportions of temporal and masking reports showed a similar course over the SOA as was reported before (Reeves, 1982; Koster et al., 2020; Kraut & Albrecht, 2022). In addition, they are in line with the dual process theory (Reeves, 1982) according to which masking results from temporal integration and segregation failing at the same time. Whereas the strength of the temporal integration process is maximal in short SOA and continuously declines with increasing SOA, the temporal segregation process shows an inverse course. Thus, the temporal integration and segregation processes are equally weak in medium SOA rendering it especially likely that both processes fail at the same time so that masking results. This theoretical prediction fits nicely to our results since the intersection of the average proportion of the temporally integrated and segregated courses as well as the peak masking proportion coincide in the same SOA. Compared to our previous study (Kraut & Albrecht, 2022) the proportion of masked percepts were substantially lower in the current study (20% vs. 40%). This is probably due to shorter presentation durations of the mask in the current study (30 ms vs. 120 ms).

4.2 Neural correlates and sources of temporal integration and segregation

4.2.1 Phase differences

The pre-stimulus phase differences in the alpha and theta frequency band replicate our previous findings (Kraut & Albrecht, 2022) and demonstrate that the phase state in lower neural frequency bands is relevant for the perceived temporal integration and segregation of successively presented visual stimuli

(Samaha & Postle, 2015; Milton & Pleydell-Pearce, 2016; Ronconi et al., 2017; Ronconi & Melcher, 2017). Phase differences in the alpha frequency band have also been demonstrated to be relevant in visual masking and conscious perception (Mathewson et al., 2009; Busch et al., 2009). Thus, our findings are in line with approaches that see temporal integration and segregation as crucial components of masking (e.g., Reeves, 1982; Francis & Cho, 2008; Wutz, Weisz, Braun, & Melcher, 2014; Albrecht & Mattler, 2012, 2016; Koster et al., 2020) or that propose that lower frequency bands periodically manipulate the excitability of the underlying neural substrate thereby generating an oscillation between better and worse neural processing. This in return would affect temporal processing either through a better or worse temporal representation of the stimulus presentation (Milton & Pleydell-Pearce, 2016), a faster or slower passing of the perceptual threshold for each stimulus in the presentation (VanRullen, 2016a) or the generation of temporal integration windows around the time point of maximum excitability (Varela et al., 1981).

Our alpha and theta phase differences extend from occipital to temporal and frontal areas. Although each of these brain areas may produce its own neural oscillations, it may be possible that a travelling wave of alpha and theta activity starts in occipital brain regions and propagates the neural hierarchy bottom-up thereby keeping the original time code throughout neural processing. Such travelling waves have been demonstrated for the alpha frequency band (Fellinger, Gruber, Zauner, Freunberger, & Klimesch, 2012; Lozano-Soldevilla & VanRullen, 2019) and explain the P3 effect in the missing element paradigm (Vanbecelaere, Leeuwen, Akyürek, & Alexander, 2019). The anterior temporal brain area of the right hemisphere has been especially implicated in the alpha and theta phase differences in our study. It represents a hub for domain-general semantic knowledge (Wong & Gallate, 2012) and can be subdivided into a hierarchy of neural areas that process increasingly complex and domain-general information (Peelen & Caramazza, 2012; Bonner & Price, 2013). Accordingly, both the perceptual as well as the conceptual temporal representation of the target-mask sequence may be determined in the anterior temporal brain areas. This would be in line with the model of two visual systems (Goodale & Milner, 1992, 2008) and the idea that sensory representations are generated in the ventral stream.

Replicating pre-stimulus beta phase differences between temporally integrated and segregated reports from our previous study (Kraut & Albrecht, 2022) is an especially important finding since they have not been associated with temporal processing in the visual domain before. However, beta phase differences have been implicated in the somatosensory (Baumgarten et al., 2015) and auditory domain (Fujioka et al., 2012; Arnal et al., 2015) before. It remains an open question in which way beta oscillations influence temporal processing and whether they themselves alter the excitability of the neural substrate. Eventually, phase differences in multiple frequency bands have been proposed to reflect multiple integration windows that operate in parallel (Ronconi et al., 2017).

The localization of beta phase differences differed from the localization of theta and alpha phase differences speaking against identical mechanisms in different frequency bands. At around 450 ms before stimulus presentation beta phase differences were localized in the left dorsolateral prefrontal cortex and spread to temporal brain areas of the right hemisphere around 350 ms before stimulus presentation. The left dorsolateral prefrontal cortex has been associated with a variety of high-level executive functions like top-down attentional control

(MacDonald, Cohen, Stenger, & Carter, 2000) and perceptual decision making (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006). These executive functions may be realized by representing abstract task properties (rules and task sets) that bias the local competitive activations of neural areas further down in the hierarchy (Desimone & Duncan, 1995; Miller, 2000; Braver, Cohen, & Barch, 2002). Such a bias may be especially relevant for ambiguous stimulus configurations as our target-mask sequence. The beta frequency band may represent the neural transmitter frequency that passes this bias from frontal brain areas to brain areas further down in the neural hierarchy. This is supported by findings demonstrating a beta phase coherence between frontal and parietal areas that was associated with contour integration (Castellano, Plöchl, Vicente, & Pipa, 2014) and the top-down deployment of attention (Buschman & Miller, 2007). Thus, our findings fit a pre-stimulus top-down influence of frontal areas on temporal areas via beta oscillations.

The brain regions identified in the current study overlap largely with regions that have been associated with visual masking in fMRI studies. Similar to our proposed top-down influence of the beta frequency band on temporal processing, frontal brain regions have also been implicated in metacontrast and backward masking (Haynes et al., 2005, Imamoglu et al., 2014). Such effects in frontal brain areas likely reflect top-down (attentional) processes modulating the masking effect (Boyer & Ro, 2006). Moreover, and similar to our proposed bottom-up influence of the alpha and theta frequency band on temporal processing, occipito-temporal brain areas have also been implicated in masking (Haynes et al., 2005; Mathewson et al., 2009; Railo et al., 2011; Imamoglu et al., 2014). Especially an interruption of the occipito-temporal communication was found to be essential for the masking phenomenon to occur (Haynes et al., 2005; Imamoglu et al., 2014). Beyond that, we found phase differences in further brain areas that have also shown to correlate with the masking function, like the putamen, the cingulate gyrus and the insula (Albrecht et al., 2013).

Unexpectedly, we also observed phase differences between reports of integrated and segregated percepts in the supplemental motor area, the basal ganglia and the cerebellum, all of which are traditionally associated with motor control. These brain areas, however, have also been associated with temporal processing before (Rao, Mayer, & Harrington, 2001). Specifically, both the supplemental motor area and the basal ganglia have been associated with a time-keeping mechanism (Wittmann, 1999; Ferrandez, Hugueville, Lehéricy, Poline, Marsault, & Pouthas, 2003). Accordingly, patients with Parkinson's disease, and hence an impaired functioning of the supplemental motor cortex and basal ganglia, show an impaired performance in temporal tasks (Harrington, Haaland, & Hermanowicz, 1998). The cerebellum in turn has also been suggested to be specialized in generating precise temporal representations and to act as a general timing device (Ivry & Keele, 1989; Mangels, Ivry, & Shimizu, 1998; Wittmann, 1999; Justus & Ivry, 2009) that is also involved in temporal perception when no motor movement is necessary (Ivry, Keele, & Diener, 1988).

Therefore, our phase differences in the supplemental motor area, the basal ganglia and the cerebellum may reflect differences in temporal processing. In our view, these phase differences are unlikely to reflect (preparatory) motor processing since (1) participants gave their reports more than one second after the phase effects, (2) participants answered always with their right hand and (3) the assignment of reports to buttons was counterbalanced over participants. Our study would hereby add to the evidence that some areas that were traditionally associated with motor control actually reflect a timing mechanism that not only finds use in motor control but also in the temporal processing of stimuli in other modalities.

4.2.2 Power differences

Although power effects would fit into the framework of explaining neural differences in temporal processing through a moderation of the excitability of the underlying neural substrate, they have not been found (Milton & Pleydell-Pearce, 2016). The authors of this study proposed that the alpha phase reflects a fundamental periodicity in the thalamocortical information transfer that is independent from power effects. Thus, our theta power differences in hippocampal brain areas of the left hemisphere may not reflect differences in temporal processing. Nonetheless, the theta frequency band has been demonstrated to be integral for the hippocampal brain region and mnemonic functioning (see for example Kirk & Mackay, 2003 or Vertes, 2005). Since the theta power in the hippocampus was associated with both the novelty and familiarity of stimulus properties (Strange, Fletcher, Henson, Friston, & Dolan, 1999), this power difference may reflect an imbalance in the total number of temporal reports that were given by most participants before equalizing them. We want to refrain from more speculative interpretations of this effect since only one voxel-time-frequency combination showed this effect significantly.

4.2.3 ERF differences

Our first ERF differences occurred 385 ms after target onset and showed a greater neural activation for temporally integrated reports. Both the timing of the effect and its direction are in accord with the contour integration negativity (Pitts & Martinez, 2014) that we have also demonstrated in our previous study (Kraut & Albrecht, 2022). Perceiving the target and mask stimuli temporally integrated induces more contours since a small white gap between both stimuli as well as four small white triangles are created in the interior of the mask that are not filled in by the target. Since these contours are not created in a temporally segregated perception, contour integration processes may be more engaged for a temporally integrated perception of the target-mask sequence. An increased neural activation for trials with a successful temporal integration has also been reported for the missing element task in the time range of the contour integration negativity (Akyürek, Schubö, & Hommel, 2010). Experiments on contour integration used single displays of low-level stimuli and located the origin of the contour integration negativity in occipital brain areas (Pitts & Martinez, 2014). In comparison, we may have demonstrated a contour integration negativity as late as in temporal brain areas probably because differences in contours only arise when (1) the processing of both the target and mask stimulus has finished and (2) both stimuli are then temporally integrated with each other.

Further ERF differences occurred at around 510 and 640 ms after target onset and also showed a greater neural activation for temporally integrated reports. Both effects were localized in frontal areas of the left hemisphere. Temporal effects as late as this have not been associated with stimulus processing but the differential engagement of processes to maintain a temporally integrated compared to a temporally segregated stimulus representation in working memory (Akyürek et al., 2010). The frontal localization of our ERF effects may reflect an increased engagement of executive processes in maintaining a temporally integrated representation in working memory.

4.3 Future research and limitations

Overall, our findings point out that temporal and masking effects may at least partially share the same neural sources. However, this conclusion has to be treated with caution due to substantial differences in the methodology to measure brain activity between our and previous studies. While we used a MEG and demonstrated phase differences in brain oscillations, previous studies used a fMRI and demonstrated differences in the BOLD signal. Thus, although temporal and masking effects may share the same neural sources, the specific mechanisms may differ. Further multi-methodological research is needed to gain a more precise picture of the specific mechanisms in operation. To further clarify the relationship between masking and temporal processes, we propose to concurrently investigate temporal integration, temporal segregation and masking percepts under physically identical presentation conditions and assess all three percepts on a trial-by-trial basis. In this way, it would be possible to investigate the relationship between temporal and masking mechanisms and evaluate Reeves' (1982) proposal that masking results from temporal integration and segregation failing at the same time.

Prior to performing any inferential statistics, we projected all signals into source space. To do so, we affinely transformed a template MRI volume to each participant's estimated head shape model. However, this transformation does not account for all individual differences in the brain structure and hence lacks spatial precision especially when compared to a potential recording of the structural MRI of each participant. In addition, to maintain reasonable analysis time, we determined the sources of our neural effects with a voxel size of 15 mm thereby further reducing the spatial precision of our source localization. Nevertheless, our rather coarse source localization procedure was still sufficient to locate the main neural hubs associated with temporal processing in the metacontrast masking paradigm. To reduce the number of brain areas that are implicated to partake in the generation of temporal effects, a more fine-grained source localization procedure would be needed.

4.4 Conclusion

We demonstrated that pre-stimulus phase states in both lower and higher frequency bands are associated with temporal processing in the metacontrast masking paradigm and thereby replicate our previous findings with a similar paradigm (Kraut & Albrecht, 2022). Especially temporal brain areas in the right hemisphere seem to be essential for the integration of top-down and bottom-up neural activity that prepares the neural system for the upcoming stimulus presentation. Whereas bottom-up activity was associated with the theta and alpha frequency bands, top-down activity was associated with the beta frequency band. ERF differences were, inter alia, localized in the temporal brain area of the right hemisphere and likely indicate an increased engagement of contour integration processes with a temporally integrated compared to a temporally segregated percept of the target-mask sequence. Overall, our study adds to the sparse evidence of localizing the neural correlates of temporal processing and constitutes the first study to do so using a metacontrast masking paradigm and subjective temporal reports. We thereby also demonstrate that brain regions that have not been traditionally associated with temporal processing, like the basal ganglia or the cerebellum, may partake either in the formation or evaluation of temporal percepts.

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Figure captions

Figure 1. **(a)** Depiction of the metacontrast masking stimuli and their sizes. The diamond target resulted from rotating the square target by 45°. **(b)** Schematic depiction of the course of one trial. Participants reported after each trial whether they perceived the target-mask sequence as either *simultaneous*, *temporally segregated* or no target at all and hence as *mask only*.

Figure 2. Depiction of the grand-average ***(a)*** and individual ***(b)*** courses of report proportions. Report proportions sum up to 1 in each SOA. Shaded areas in ***(a)*** reflect the between-subject standard deviation. The *primary SOA* is indicated in each individual plot by a black vertical line and its value under the x axis. Participant numbers are displayed on top of each individual plot whereby the asterisks indicate participants that were included in the MEG analyses.

Figure 3. Depiction of the three clusters of significant ERF differences whereby each column corresponds to one cluster of significant ERF differences. ***First line:*** TFCE scores in source space that were additionally averaged over all significant time points of the cluster. Voxels with a significant ERF difference are colored in white. For each cluster, the following brain areas were identified: ***(a)*** **T**: superior (R) and middle (R) temporal pole, middle (R) and inferior temporal (R); ***(b)*** **F**: middle (L), medial superior (L) and superior frontal (L); ***(c)*** **F**: middle (L), superior medial (L) and superior frontal (L). ***Second line:*** time-course of TFCE scores that were additionally averaged over all significant voxels of the cluster. The dashed

line indicates the significance threshold. Areas that are shaded in grey reflect a cluster's significant time interval. ***Third line:*** time-course of the grand-average ERF values that were additionally averaged over all significant voxels of the cluster.

Figure 4. Depiction of the single cluster of significant power differences. All clusters are labelled so that they can be matched in source and time-frequency space. ***First line:*** TFCE scores in source space that were additionally averaged over all significant time-frequency points of a cluster. Whereas positive values depict voxels with a greater power for *simultaneous* reports, negative values depict voxels with a greater power for *temporally segregated* reports. Voxels with a significant power difference are colored in white. For each cluster, the following brain areas were identified: ***(a)*** **T**: parahippocampal (L), hippocampus (L). ***Second line:*** time-frequency space indicating the number of voxels for which a certain time-frequency combination became significant. Whereas positive values indicate the number of voxels with a significantly greater power for *simultaneous* reports, negative values indicate the number of voxels with a significantly greater power for *temporally segregated* reports. Shaded areas depict time-frequency combinations which may have been influenced by post-target activity. Boxes indicate clusters of time-frequency combination that were chosen for closer inspection in source space.

Figure 5. Depiction of four clusters of significant POS differences. All clusters are labelled so that they can be matched in source and time-frequency space. ***Upper***

left corner: Time-frequency space indicating the number of voxels for which a certain time-frequency combination showed a significant phase shift. Boxes indicate clusters of time-frequency combinations that were chosen for closer inspection in source space. ***Lower left corner and right column:*** TFCE scores in source space that were additionally averaged over all significant time-frequency points of a cluster. Voxels with a significant phase difference are colored in white. For each cluster, the following brain areas were identified: ***(a)*** **C**: cerebellum 6 (R), 8 (R/L), 9 (R/L), crust1 (R); **T**: inferior (R/L), middle (R/L) and superior (R) temporal, middle (R/L) and superior (R/L) temporal pole, fusiform (R), parahippocampal (R), hippocampus (R); **O**: inferior occipital (R), lingual (R), **I**: insula (R), rolandic oper (R); **BG**: putamen (R), caudate (R), pallidum (R); **(b) C**:cerebellum 4 (R), 5 (R), 6 (R/L), 8 (R), 9 (R), crust2 (L), vermis 4, 5, 6, 7; **O**: lingual (R/L), calcarine (R/L); **BG**: caudate (R); **PC**: precuneus (R); **Cng**: middle (R) and posterior (R) cingulum; **M**: precentral (R), postcentral (R); **F**: middle (R) and superior (R) frontal; **(c) T**: middle (R) and superior (R) temporal, superior temporal pole (R), fusiform (R), parahippocampal (R), hippocampus (R); **BG**: putamen (R), caudate (L); **I**: insula (R/L); **Cng**: anterior (L) and middle (L) cingulum; **M**: supplemental motor area (L); **F**: middle frontal (L), inferior triangular frontal (L); **(d) T**: inferior temporal (R), middle (R) and superior (R) temporal pole.

Figures

Figure 1

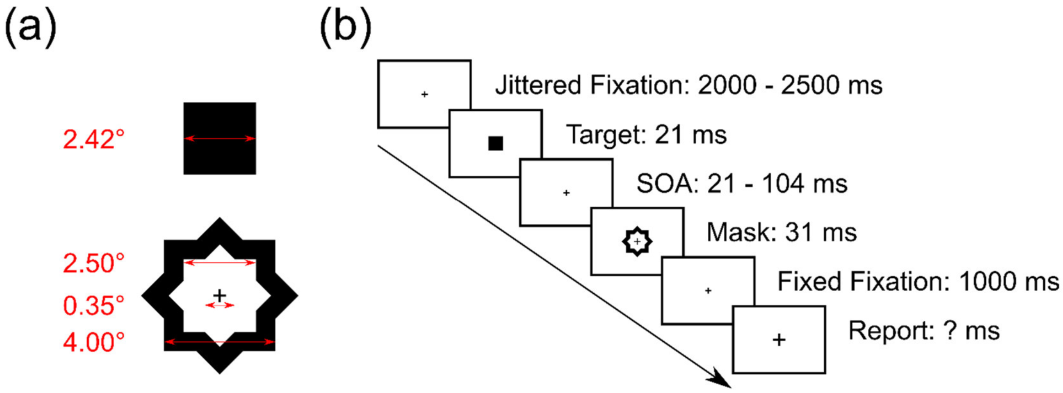


Figure 2

Figure 3

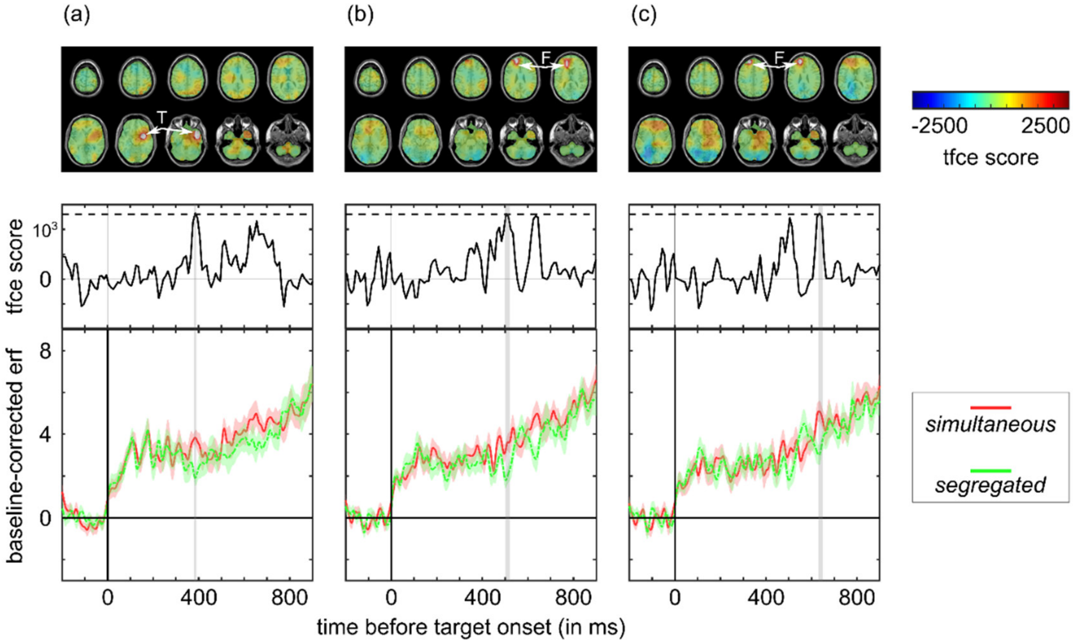

(a)
(b)
(c)
T
F
F
-2500
2500
tfce score
tfce score
10^3
0
baseline-corrected erf
8
4
0
0
400
800
time before target onset (in ms)
simultaneous
segregated

Figure 4

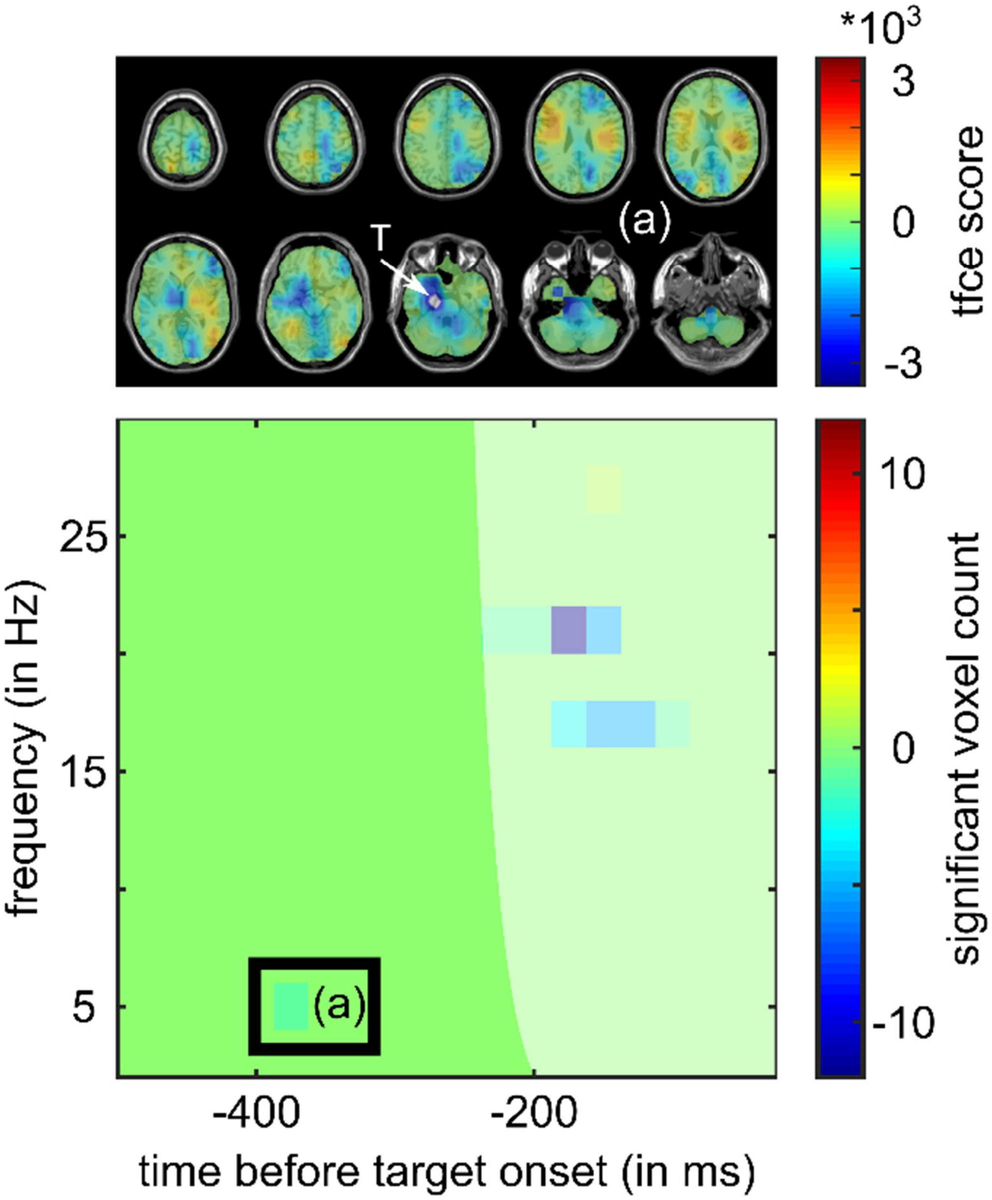
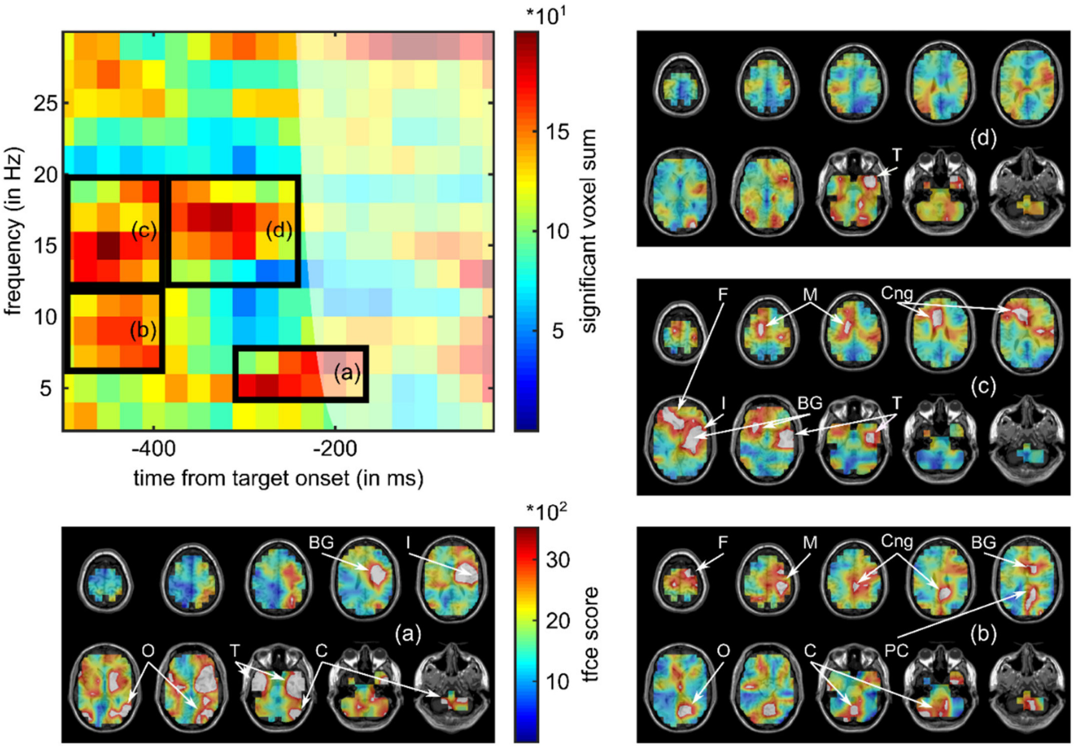

*10^3
3
0
-3
tfce score
T
(a)
25
15
5
frequency (in Hz)
-400
-200
time before target onset (in ms)
(a)
10
0
-10
significant voxel count

Figure 5


*10^1
25
20
15
10
5
frequency (in Hz)
(c)
(d)
(b)
(a)
-400
-200
time from target onset (in ms)
15
10
5
significant voxel sum
*10^2
30
20
10
tfce score
T
(d)
F
M
Cng
(c)
I
BG
T
BG
I
(a)
O
T
C
F
M
Cng
BG
(b)
O
C
PC

Appendix III - manuscript for study 3

Kraut, A. T., & Albrecht, T. (2022). *Neural correlates of temporal and masking processes: a concurrent investigation in a multi-paradigm study* [Unpublished manuscript]. Department of Experimental Psychology, University Göttingen.

Manuscript title

Neural correlates of temporal and masking mechanisms: a concurrent investigation in a multi-paradigm study

Short title

Neural correlates of temporal and masking mechanisms

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Abstract

Although research on temporal and masking mechanisms share theoretical and empirical similarities, their fields of research show nearly no overlap. This is especially curious since both mechanisms have been postulated to be relevant for the respective other field of research. Accordingly, we present the first study with a concurrent investigation of temporal and masking mechanisms. We conducted a metacontrast masking experiment and asked participants to report whether they perceived the target-mask sequence temporally integrated, segregated or masked and compared the ERP of each report category against each other. In addition, to estimate the degree of shared processes between paradigms that investigate temporal mechanisms, we also conducted a missing element and two-flash task with the same participants and compared the ERP of correct and incorrect reports against each other. For the metacontrast masking task, our findings demonstrated a visual awareness negativity and a late positivity for a comparison of both temporally integrated and segregated reports against masked reports. In addition, we found a contour integration negativity for the comparison of both temporally integrated and masked reports against temporally segregated reports. Our findings support theories that postulate the relevance of contour processes in the masking phenomenon and emphasize the relevance to distinguish between different phenomenal percepts when investigating the masking phenomenon. A significant relationship between the behavioral data of the metacontrast masking and missing element task indicated a shared mechanism which according to their neural data may constitute a masking mechanism.

1. Introduction

Due to the complexity of our neural system, different fields of research have specialized in the exploration of one particular aspect of it. This partitioning, however, is man-made and allows for different fields of research to develop in parallel while at bottom they investigate the same underlying aspect of the neural system. We propose that the research fields on temporal and masking mechanisms constitute one such example. Both fields of research use highly similar paradigms in which two brief stimuli are presented in succession and have produced similar neural correlates. Moreover, while temporal processes have been suggested to play a role in masking paradigms (Reeves, 1982; Francis & Cho, 2008; Jannati & Di Lollo, 2012; Sackur, 2012; Koster, Albrecht, & Mattler, 2020; Kraut & Albrecht, 2022; Kraut, Sandberg, & Albrecht, 2022), masking processes have been suggested to confound temporal paradigms (Akyürek & Wijnja, 2019; Kraut & Albrecht, 2022). Against this background, we propose that both fields of research would profit from a unification and hence present the first study with a concurrent investigation of the neural correlates of both temporal and masking mechanisms.

1.1 Research on masking mechanisms

In vision research, masking describes the reduction of the visibility of a target stimulus through the presentation of a masking stimulus either before (forward masking) or after (backward masking) the presentation of the target stimulus (Breitmeyer & Ögmen, 2000; Breitmeyer & Ögmen, 2006). A special form of backward masking is metacontrast masking is in which the mask is not only presented after the target but does also not spatially overlap with it. One of the strongest parameters that influences the extent of the target's reduction in visibility is the time that passes between the onset of the target and the mask presentation, the so-called stimulus onset asynchrony (SOA). As a function of the SOA; the reduction of the target's visibility follows a U-shaped course meaning that the masking effect is strongest in medium SOA (~ 50 ms) and lowest in short and long SOA. This so-called masking function challenges masking theories and demands an answer to the question why especially medium SOA result in the maximum reduction of the target's visibility.

Most theories on visual masking assume that the processing of the mask intervenes a critical phase of the target's processing thereby reducing its visibility. One of the most successful theories to explain the masking phenomenon is the dual-channel, sustained-transient approach (Kulikowski & Tolhurst, 1973; Tolhurst, 1973) and its later update the neural network model of retino-cortical dynamics (RECOD; Ögmen, 1993; Breitmeyer & Ögmen, 2000). According to both theoretical approaches, object processing takes place in two types of channels. While object features are processed in slow-paced sustained channels, coarse patterns like the spatial localization and movement of a stimulus are processed in fast-paced transient channels. Masking is explained as an inter-channel inhibition in which the transient activity of the mask inhibits the sustained activity of the target. An alternative approach to explain the masking phenomenon constitutes the *boundary contour and feature contour system* (Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994). The core idea behind this approach is that the contours of a stimulus need to be processed in order for its surface to be filled in (Breitmeyer & Jacob, 2012). Masking is induced through a lateral inhibition of those cells that process the target's contours through neighboring cells that process the contours of the mask (Francis, 1997). In medium

SOA, the erosion of the target contours has already started and is especially susceptible to the lateral inhibition of the mask thereby resulting in a maximum masking effect.

In the framework of both the RECOD and the BCS/FCS models, the masking function was solely associated with changes in the visibility of the target over the course of the SOA. However, individual masking functions have been demonstrated to result from an individual weighing of multiple processes (Albrecht & Mattler, 2016). In addition, a masked percept is only one out of several possible phenomenal percepts that occur in metacontrast masking and shape the masking function (Koster et al., 2020). In this study, all phenomenal percepts could be grouped as either percepts that are related to the target contrast, motion or the temporal order of the target-mask sequence. Temporal processes have repeatedly been proposed to play a crucial role in metacontrast masking (Reeves, 1982; Francis & Cho, 2008; Jannati & Di Lollo, 2012; Sackur, 2012; Koster et al., 2020; Kraut & Albrecht, 2022; Kraut et al., 2022). This becomes especially evident since the target-mask sequence is regularly reported to be perceived simultaneously despite they are never concurrently visible on the screen. In sharp contrast to models that try to explain the masking function with a masking process, Reeves' (1982) dual process theory is based on two independent temporal processes. In this model, the strength of a temporal integration process decreases with increasing SOA while that of a temporal segregation process increases. Consequently, both temporal processes are equally weak in medium SOA and hence the likelihood of both of them failing at the same time is maximal here. Such a concurrent failure of both temporally integrating and segregating the target-mask sequence is postulated to incur masking. This hypothesis has not been tested yet.

One way to test this hypothesis would be to determine the neural correlates of temporal integration and segregation in metacontrast masking and demonstrate that in their absence masking results. However, masking and temporal mechanisms have never been concurrently investigated. Until recently, research on the neural correlates of the masking phenomenon has been limited to a comparison between trials with a masked and unmasked perception of the target. This comparison indicated that an unmasked perception of the target was associated with more negative amplitudes in the N1-N2 time range and occipito-temporal electrodes (Railo, Koivisto, & Revonsuo, 2011; Förster, Koivisto, & Revonsuo, 2020). This so-called visual awareness negativity (VAN) was associated with processes in the ventral stream that engage in the emergence of conscious visual percepts. The VAN is usually followed by the late positivity (LP) that depicts a more positive amplitude in the P3 time range and centro-parietal electrodes for trials with an unmasked perception of the target. However, the LP has been linked to post-perceptual processes in working memory (van Aalderen-Smeets, Oostenveld, & Schwarzbach, 2006; Railo et al., 2011) and the global workspace (Del Cul, Baillet & Dehaene, 2007) and is hence not directly related to the emergence of conscious visual percepts itself.

1.2 Research on temporal mechanisms

Similar to the metacontrast masking task, paradigms to investigate temporal integration and segregation processes have been focusing on the presentation of a quick succession of two brief stimuli. Though there have been recent ambitions to concurrently investigate temporal integration and segregation processes (Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016; Wutz, Melcher,

& Samaha, 2018), they have usually been investigated separately from each other.

A popular paradigm to investigate temporal integration processes is the missing element task (e.g. Hogben & Di Lollo, 1974; Akyürek, Schubö, & Hommel, 2010; Wutz et al., 2016; Wutz et al., 2018). In this task, a grid with the same number of rows and columns is generated and all of its positions despite one filled with the same visual stimulus. The occupied positions of this grid are then evenly distributed among two grids that are identical in construction as the first one. Participants are presented with a brief and successive presentation of both grids and asked to report the missing element; that position that was neither occupied in the first nor the second grid. Findings indicate that participants are more likely to correctly identify the missing element the shorter the ISI between the grids becomes which is usually attributed to a successful temporal integration of both grids.

Correct identifications of the missing element have been associated with a more negative amplitude in the N1, N2 and early P3 time window and a more positive amplitude in the late P3 time window (Akyürek et al., 2010; Akyürek & Meijerink, 2012). The authors interpreted the N1 effect as one of the earliest neural correlates of feature integration. However, a later study on the missing element task could not replicate the N1 effect (Akyürek & Meijerink, 2012). In addition, since a more negative amplitude in the N1 time range has not only been associated with successful temporal integrations in the missing element task but also successful temporal segregations in the two-flash task (Ronconi, Oosterhof, Bonmassar, & Melcher, 2017), it is questionable whether effects on the N1 reflect temporal mechanisms. Besides the effect on the N1, effects on the N2 and early

P3 were associated with a spatial integration mechanism that is more engaged as a result of a successful temporal integration of both grids. This finding bears resemblance with the contour integration negativity (CIN; Pitts & Martinez, 2014) which reflects a more negative amplitude for stimuli whose segments form contours. A temporally integrated perception of both grids in the missing element task induces more contours since all visual elements in the grid are simultaneously processed. Thus, contour integration processes may be more engaged for a successful temporal integration in the missing element task. Eventually, effects on the P3 were suggested to reflect a differential engagement of a consolidation processes in visual memory since a temporally integrated perception of both grids requires the consolidation of only one grid compared to two grids. Such an interpretation is in line with previous findings showing more negative P3 amplitudes the more stimuli needed to be kept in visual memory (Vogel & Machizawa, 2004).

A popular paradigm to investigate temporal segregation processes is the two-flash task (e.g. Exner, 1875; Samaha & Postle, 2015; Milton & Pleydell-Pearce, 2016; Ronconi & Melcher, 2017). In this task, two brief visual flashes are presented successively at the same place in the periphery and participants are asked to report whether they perceived one or two flashes. Findings indicate that participants are more likely to correctly perceive two-flashes the longer the ISI between them becomes which is usually attributed to a successful temporal segregation.

ERP differences in the two-flash task are limited to a N1 effect showing more negative amplitudes for trials with a successful temporal segregation of the flash presentation (Ronconi et al., 2017). As described before, this effect is unlikely to reflect temporal processing since it has been associated with both successful temporal segregations in the two-flash task and successful temporal integrations in the missing element task (Akyürek et al., 2010).

A potential problem of most paradigms that investigate temporal mechanisms is their explicit or implicit assumption of a temporal antagonism meaning that an unsuccessful temporal integration is automatically equated to a successful temporal segregation and vice versa (see e.g. Samaha & Postle, 2015; Wutz et al., 2016; Milton & Pleydell-Pearce, 2016; Ronconi et al., 2017, Ronconi, Busch, & Melcher, 2018; Sharp, Melcher, & Hickey, 2019). To solve the missing element task, it is undisputed that both grids need to be successfully temporally integrated. However, a temporal segregation of both grids is only one of several processes whose success would render the missing element task nearly impossible to solve. A masking process for example may reduce at least partially the visibility of the first (backward masking) or second grid (forward masking) rendering the detection of the missing element much more difficult. Such a masking confound in the missing element task has been suggested previously (Akyürek & Wijnja, 2019; Kraut & Albrecht, 2022) but has not yet been investigated. The same argumentation holds true for the two-flash task. Although it is undisputed that a successful temporal segregation is needed to rightly perceive two flashes, both a successful temporal integration and a masking of one of the flashes due to the presentation of the other flash may explain the perception of only one flash. All in all, to further investigate a potential masking confound in temporal paradigms a concurrent investigation of bot temporal and masking processes would be needed.

1.3 A concurrent investigation of temporal and masking mechanisms

As a first step towards a concurrent investigation of both temporal and masking mechanisms, we conducted two studies that investigated the neural correlates of temporal integration and segregation in a metacontrast masking task (Kraut & Albrecht, 2022; Kraut et al., 2022). In both studies, we asked participants to evaluate on each trial whether they perceived the target-mask sequence temporally integrated, temporally segregated or no target at all while their neural activity was recorded with an EEG or MEG. We contrasted the neural activity between trials with a temporally integrated and segregated report and, inter alia, demonstrated a more negative amplitude for trials with a temporally integrated report from 200 to 450 ms after target presentation in centro-parietal electrodes. Due to its similarity with the CIN (Pitts & Martinez, 2014), a temporally integrated perception of the target-mask sequence may engage contour integration processes more than a temporally segregated perception. In addition, our effect is in accord with the N2 and early P3 effects reported in the missing element task (Akyürek et al., 2010; Akyürek & Meijerink, 2012) that we have also previously associated with the CIN. Overall, an increased engagement of a contour integration process as a consequence of a prior successful temporal integration may indicate a shared temporal processing characteristic in the metacontrast masking and missing element task.

Based on our evidence that temporal mechanisms are active in metacontrast masking, we designed our current study to be the first to concurrently investigate the neural correlates of temporal and masking mechanisms. To do so, we asked participants on each trial of a metacontrast masking task to report whether they perceived the target-mask sequence temporally integrated, temporally segregated or masked and then compared the neural activities between each report category. A concurrent investigation of temporal and masking phenomena allowed us to explore their relationship and to test Reeves' (1982) proposal that masking results in the absence of any temporal processing. Moreover, since the investigation of the neural correlates of masking has been limited to performance-based approaches, we were the first to test whether a phenomenally perceived masking induces the same neural correlates. This was especially interesting since performance-based approaches have always been comparing masked trials with unmasked trials that constituted an undefined mixture of temporally integrated and temporally segregated perceptions of the target-mask sequence.

In addition, to further investigate the degree of shared temporal processes between paradigms and explore the notion that the missing element and two-flash task may be confounded by a masking process, we recorded the neural activity of our participants not only for a metacontrast masking task but also for a missing element and two-flash task. A multi-paradigm study has the advantage that the data of each paradigm can be directly related to each other since the same participants contribute data to each of them. Thus, assuming that the missing element and two-flash task are unconfounded by a masking process, a comparison of the neural activity between correct and incorrect trials should not result in effects that are also observable for a comparison of masked and unmasked reports in the metacontrast masking task.

Alongside post-stimulus differences in the event-related potentials, pre-stimulus phase and power effects have been repeatedly been associated with both temporal and masking mechanisms. A theoretical discussion of these effects as well as preliminary results of our time-frequency analysis can be found in the supplements to this paper.

1.4 Adapting report proportions of temporal and masking percepts

When comparing the neural activity of different report categories against each other, it is essential that each report category depicts a sufficient number of trials and that the comparison is unconfounded by physical presentation parameters. Thus, it has become standard practice in vision research to refine for each participant one physical presentation condition for which each report category is reported equally often and to then predominantly present trials with this condition (Busch, Dubois, & VanRullen, 2009; Wutz et al., 2016; Ronconi et al., 2017). Although a variation of the SOA can be used to influence the report proportions of both temporal and masking percepts, it is rare that the SOA that depicts an equal report proportion of temporal integration and segregation percepts coincides with the SOA for which a sufficient amount of masking is reported. Since it is intuitive to vary the SOA to influence the report proportion of temporal percepts, we decided to additionally vary the mask size to influence the report proportions of masking percepts. Several parameters that influence the energy ratio between the target and mask (Weisstein, 1972) have been demonstrated to influence masking proportions, like the mask duration (Breitmeyer, 1978), the target-mask distance (Cox, Dember, & Sherrick, 1969) or the mask size (Kao & Dember, 1973). However, since most of these results are based on a low number of participants and performance-based measures, it was unclear to which degree these results will generalize to our phenomenological approach and which parameters will be suited for a fine tuning of perceptual report proportions.

We therefore conducted a series of piloting studies of which a systematic variation of the mask size was the most promising one. The core idea of this study was that a manipulation of the mask size can be realized by manipulating either the mask's edge size, the mask's thickness or the target-mask distance. By manipulating one of these parameters, one further parameter automatically needed to change too while the third parameter could be kept constant. Thus, in a systematic variation of these parameters of the mask size, we found that an increase of the mask's edge size and mask's thickness while keeping the target-mask distance constant worked best to consistently increase the report proportion of masked reports. Using this manipulation, we found for all six of our participants at least one combination of SOA and mask size for which temporally integrated, temporally segregated and masked percepts were reported equally often. From now on, we will call this condition the optimal presentation condition (OPC). Such an OPC could only be determined for four out of six participants when the mask's edge length was kept constant and only for three out of six participants when the mask's thickness was kept constant. Against this background, we decided for our current study to manipulate the report proportions of the masked percept by keeping the target-mask distance constant. Figure 1 depicts average report proportions for each percept separately for each manipulation of the mask size. Since no masked percept was directly measured in either the missing element or two-flash task, the OPC was determined by that ISI which showed an equal amount of correct and incorrect trials.

**** Insert figure 1 here ****

Although our previous metacontrast masking studies demonstrated a high retest reliability of the OPC between sessions (*r*(13) = .86; Kraut & Albrecht, 2022) and within one session (*r*(22) = .88; Kraut, Sandberg, & Albrecht, 2022), just little variations of the OPC in the recording sessions could lead to a participant's exclusion due to too less trials in either report category. For this reason, we adapted the ISI and mask size of the OPC after each block in the recording sessions if necessary. In this way, we aimed to achieve equal report proportions of each percept in the OPC over the course of the recording sessions in each paradigm. Consequently, physical stimulation parameters could potentially vary between blocks within one participant. To still keep physical stimulation parameters constant in our analysis, we extracted the same number of trials for each percept from each block.

2. Method

2.1 Participants

57 students of the Georg-August-University Göttingen participated in this study for financial compensation. Upon their first arrival to the study, all participants gave their informed consent. 33 participants needed to be excluded over the course of the study due to scheduling conflicts (*n* = 3), technical problems (*n* = 2) or since no optimal SOA and mask size could be determined in the second (*n* = 15), third (*n* = 5) or fourth (*n* = 8) session of the metacontrast masking task. Thus, 24 participants (15 female, 9 male) between 18 and 29 years old (*M* = 23.1, *SD* = 2.9) were included into the final analyses for the metacontrast masking task. Two additional participants needed to be excluded after the metacontrast masking sessions due to scheduling conflicts (*n* = 1) and technical problems (*n* = 1).

Thus, 22 participants (14 female, 8 male) between 18 and 29 years old (*M* = 23.0, *SD* = 3.0) were included into the final analyses for the missing element and two-flash task. All participants reported to be right-handed and to have normal or corrected to normal vision.

2.2 Paradigms

This study comprised seven sessions of which the first four sessions were dedicated to the metacontrast masking task and the last three session to the missing element and two-flash task. Each task was initially trained before an EEG recording took place. For the metacontrast masking task, the first and second session were used for training and the third and fourth session were used for the EEG recording. For the missing element and two-flash task, the fifth session was used for training and the sixth and seventh sessions were used for the EEG recording. We counterbalanced over participants whether the EEG recording of the missing element or the two-flash task took place in the sixth or seventh session.

All experiments were run on a 19'' monitor with a refresh rate of 160 Hz and a screen resolution of 640x480 pixels. Stimulus presentation was controlled by Presentation® (Version 18.1, Neurobehavioral Systems, Inc.). Each paradigm at hand was explained in the beginning of each session. To check for task understanding, each participant had to describe the task and its different report categories in their own words before starting it and report on their task strategies after each session.

2.3 Metacontrast masking task

2.3.1 Stimuli

All stimuli in the metacontrast masking task were presented with full contrast (Michelson contrast = 100 %) in black (0.03 cd/m^2) on a white background (84.4 cd/m^2). Both target and mask stimuli consisted of a square shaped stimulus. While the target's interior was filled, the mask's interior was cut out so that the target could fit snuggly inside. The size of the mask was varied by further extending or shrinking its outer contour. The mask's inner contour did not change to keep the spacing between target and mask constant at all mask sizes. Figure 2a depicts all stimuli and their sizes.

**** Insert figure 2 here ****

2.3.2 Task

After each trial, participants were asked to report on their phenomenal perception of the target-mask sequence that is depicted in figure 2a. Participants were able to report either of four phenomenal percepts and were told to report the most applicable one if they had an ambivalent percept. A *simultaneous* percept should be reported if the target was visible and appeared inside of the mask as one event. A *segregated* percept should be reported if the target was visible and appeared temporally before the mask as two events. In cases in which the target was not visible at all, participants could either indicate that they perceived only the mask as one or two events. We added the later report option for exploratory analysis since participants have reported to perceive no target but a sequence of two masks in previous experiments. For our current analysis, however, all trials in which the target was reported to not be visible were categorized as an *only mask* percept. Reports were made without any time constraint and by pressing one of four buttons on the keyboard (F1 to F4 on a keyboard turned upside down) that were assigned to the index, middle, ring, and little finger of the right hand. The assignment of buttons to report categories was counterbalanced over participants. It was emphasized that participants should try to keep their gaze on the fixation point and to refrain from blinking for the whole trial duration.

2.3.3 Procedure

The general trial sequence (figure 2a) for the metacontrast masking paradigm was the same for all sessions. All stimuli were presented in the center of the screen. Each trial began with a fixation dot that was presented between 1000 and 2000 ms (160 to 320 frames) thereby rendering the following target onset unpredictable. The target was presented for 25 ms (4 frames) and was separated from the mask by an ISI of 0 (0 frames), 18.75 (3 frames), 31.25 (5 frames), 43.75 (7 frames), 56.25 (9 frames) or 75 ms (12 frames). The mask was presented for 31.25 ms (5 frames) and was followed by a fixation dot that was presented for 1000 ms (160 frames). Eventually, a fixation cross indicated that participants could report on their percept without any temporal constraints. The next trial started as soon as participants made their report.

The first two sessions were dedicated for training the phenomenal task without any EEG measurement so that participants would develop stable report categories for each percept. Each session comprised 756 trials organized in

9 blocks with each 84 trials. In each block, all ISI were presented equally often. While we presented a medium mask size (2.36°, 8 pixels contour size) throughout the first session, we alternated three different mask sizes between blocks in the second session (small: 2.08°, 4 pixels contour size; medium: 2.36°, 8 pixels contour size; large: 2.65°, 12 pixels contour size). For each participant, an alternation of mask sizes was determined as one out of six possible sequences of mask sizes for the first three blocks (e.g. block 1: large mask, block 2: small mask, block 3: medium mask) which was then repeated for the remaining six blocks. These alternations were counterbalanced over participants. Through varying both the ISI and the mask size, the second session was intended to find a combination of ISI and mask sizes for which all percepts were reported equally often. Possible candidates for this “optimal” presentation condition (OPC) were all combinations of ISI and mask size whereby we also included ISI that were not presented but realizable by linearly extrapolating their potential report proportions. If there was a draw between multiple combinations of ISI and mask sizes, a smaller mask size and a longer ISI were preferred. The minimum requirement for an OPC was that each percept was reported in at least 5 trials. Participants needed to be prematurely excluded after the second session, if this minimum requirement could not be met by any combination of ISI and mask size.

The third and fourth session were then dedicated to get as many trials from each report category under otherwise stable physical presentation conditions while also recording the EEG. Therefore, the previously determined OPC was presented in half of all trials. The remaining trials were equally distributed among the ISI that were already presented in the previous sessions. Each session comprised 768 trials organized in 8 blocks with each 96 trials. After each block, we assessed the validity of the OPC and adapted it if necessary in the following block to keep an equal distribution of reports for each category in OPC trials. First, we determined the need to shift the ISI of the OPC. To do so, we calculated the report proportions for *simultaneous* and *segregated* percepts in trials with an OPC presentation. If the report proportion of the *simultaneous* percept was below 16%, the ISI of the OPC was reduced by one frame (6.25 ms). In contrast, the ISI of the OPC was increased by one frame (6.25 ms) if the report proportion of the *segregated* percept was below 16%. The adaptation of the ISI was limited to a range between 0 and 75 ms. Second, we determined the need to shift the mask size. To do so, we calculated the report proportions of the *only mask* percept in trials with an OPC. If the ISI of the OPC had been shifted before, the report proportion of the *only mask* percept was linearly extrapolated if necessary. If the report proportion of the *only mask* percept was below 16%, the mask size was increased by 1 pixel. In contrast, the mask size was reduced by 1 pixel if the report proportion of the *only mask* percept was above 50%. The adaptation of the mask size was limited to a range between 1.86° (1 pixel contour size) and 2.94° (16 pixels contour size).

A new OPC for the first block of the fourth session was calculated based on all trials with an OPC presentation in the third session. Participants needed to be excluded prematurely after the third session if there was no combination of ISI and mask size for which each percept was reported in at least 5 trials and hence the minimum requirement for an OPC was not met.

2.4 Missing element task

2.4.1 Stimuli

If not otherwise indicated, all stimuli in the missing element task were presented with full contrast (Michelson contrast = 100 %) in black (0.03 cd/m^2) on a white background (84.4 cd/m^2). Stimuli were generated by randomly placing filled black squares into half of the grid positions of a previously empty 5x5 grid. For each trial, two grids were generated so that by overlaying both of them no grid position was occupied twice and only one grid position was left empty. A response display was generated by placing empty boxes in each possible grid position. All stimuli were presented inside of a fixation field that was made up of a black (23.76 cd/m^2) and lower contrast contour (Michelson contrast = 56.1%). Figure 2b depicts all stimuli and their sizes.

2.4.2 Task

In each trial, a sequence of two grids was presented (figure 2b). Participants were asked to report that grid position that was neither occupied in the first nor the second grid. Reports were made without any time constraint and with the index finger of the right hand by moving the mouse to the desired grid position in the response display and clicking on it with the left mouse button. The mouse cursor was reset after each trial to the center of the lower half of the screen and only became visible when the response grid was shown. If participants were unsure what to report, they were told to guess. It was emphasized that participants should try to distribute their attention equally in the fixation field while keeping their gaze steady and refraining from blinking for the whole trial duration.

2.4.3 Procedure

The trial sequence of the missing element task was the same in both the training and recording session (figure 2b). All stimuli were presented in the center of the screen. Each trial started with an empty fixation field that was presented for 1000 to 2000 ms (160 to 320 frames) thereby rendering the onset of the first grid unpredictable. A variable ISI of 0 (0 frames), 18.75 (3 frames), 31.25 (5 frames), 43.75 (7 frames), 56.25 (9 frames) or 75 ms (12 frames) separated the presentation of the first and second grid from each other that were each presented inside of the fixation field. Each grid was presented for 12.5 ms (2 frames). Following the second grid, an empty fixation field was presented for 1000 ms (160 frames). Eventually, the response display was presented inside of the fixation field signaling participants that they could now make their report. Participants could report without time constraints and the next trial started as soon as participants gave their report.

Whereas the training session was comprised of 252 trials organized in 3 blocks with each 84 trials, the recording session was comprised of 768 trials organized in 8 blocks with each 96 trials. All ISI in the training session were presented equally often in each block. Data of the training session were used to determine an OPC and hence one ISI for which participants reported in 50% correctly on the missing element. If there was a draw between multiple ISI, longer ISI were preferred. The minimum requirement for an OPC was that each in/correct report was reported in at least 5 trials. Participants needed to be prematurely excluded after the sixth session, if this minimum requirement could not be met by any ISI.

The OPC was presented in 50% of all trials in the recording session to get as many in/correct reports under otherwise equal physical presentation conditions. The remaining trials were equally distributed to the ISI that were already presented in the training session. The OPC was potentially adapted after each block to keep an equal distribution of in/correct reports in OPC trials. To do so, we calculated the proportion of correct reports for OPC trials. If the proportion of correct reports was lower than 31% then the ISI of the OPC was reduced by one frame (6.25 ms). In contrast, the ISI of the OPC was increased by one frame (6.25 ms) if the proportion of correct reports was larger than 69%. The adaptation of the ISI was limited to a range between 0 and 75 ms.

2.5 Two-flash task

2.5.1 Stimuli

If not otherwise indicated, all stimuli in the two-flash task were presented with full contrast (Michelson contrast = 100 %) in black (0.03 cd/m^2) on a white background (84.4 cd/m^2). Stimuli consisted of luminance-defined Gaussian blobs (*flashes)*, and were presented in black (peak value: 65.6 cd/m^2) at perceptual threshold with a reduced contrast (Michelson contrast = 12.5 %). Figure 2c depicts all stimuli and their sizes.

2.5.2 Task

In each trial, either one flash or a sequence of two flashes (figure 2c) was presented. Participants were asked to report whether they have perceived one or two flashes. Reports were made by using the same buttons on the keyboard as for a *simultaneous* (one flash) and *segregated* (two flashes) percepts in the metacontrast masking task. If participants were unsure what to report, they were told to guess. It was emphasized that participants should try to keep their gaze on the fixation point and to refrain from blinking for the whole trial duration.

2.5.3 Procedure

The trial sequence for the two-flash task was the same in both the training and recording sessions (figure 2c). Each trial began with a fixation dot that was presented for 1000 to 2000 ms (160 to 320 frames) thereby rendering the onset of the first flash unpredictable. A variable ISI of 18.75 (3 frames), 31.25 (5 frames), 43.75 (7 frames), 56.25 (9 frames) or 75 ms (12 frames) separated the presentation of the first and second flash from each other. Each flash was presented for 12.5 ms (2 frames). Unlike the fixation dot that was presented in the center of the screen, flashes were presented to the left or the right of the fixation dot in the visual periphery. After the second flash, a fixation dot was presented for 1000 ms. Eventually, a fixation cross was presented and signaled participants that they were now able to report on their perception. Participants could report without any time constraints and the next trial started as soon as participants gave their report.

Whereas the training session was comprised of 252 trials organized in 3 blocks with each 84 trials, the recording session was comprised of 768 trials organized in 8 blocks with each 96 trials. To avoid that participants might see through the task and rightly report to always perceive two flashes, we added catch trials. In these trials, the flash was also presented in the ISI thereby creating one continuous flash presentation. 16% of all trials were catch trials and each of them either used the shortest ISI of 18.75 ms (3 frames) or the longest ISI of 75 ms

(12 frames). The addition of these catch trials also opened up the possibility to check for participants’ task strategy. If participants reported to perceive two flashes only on catch trials with the shortest ISI but not the longest ISI, they would not evaluate the succession of events but the duration of overall stimulation. All ISI in the training session were presented equally often in each block and the location of the flash presentation either to the left or right of the fixation dot was balanced and randomized in each block. This balancing was done separately for catch and non-catch trials. Report proportions of non-catch trials in the training session were used to determine an OPC and hence one ISI for which participants reported in 50% correctly to perceive two flashes. If there was a draw between multiple ISI, longer ISI were preferred. The minimum requirement for an OPC was that each in/correct report was reported in at least 5 trials. Participants needed to be prematurely excluded after the sixth session, if this minimum requirement could not be met by any ISI.

The OPC was presented in 50% of all trials in the recording session to get as many in/correct reports under otherwise equal physical presentation conditions. The remaining trials were made of 29% catch trials and 71% non-catch trials with the same balancing as in the training session. The OPC was potentially adapted after each block to keep an equal distribution of in/correct reports in OPC trials. To do so, we calculated the proportion of correct reports for OPC trials. If the proportion of correct reports was lower than 31% then the ISI of the OPC was reduced by one frame (6.25 ms). In contrast, the ISI of the OPC was increased by one frame (6.25 ms) if the proportion of correct reports was larger than 69%. The adaptation of the ISI was limited to a range between 6.25 and 75 ms. The presentation of an ISI of 0 ms as in the other paradigms was avoided since this would result in the presentation of one continuous flash.

2.6 Data analyses

By potentially adapting the ISI (and mask size) of the OPC from block to block in each recording session, we ensured that each report category is reported in a sufficient number of trials under otherwise stable physical presentation conditions. In this way, however, physical presentation parameters could not be kept constant across blocks. To ensure that neural differences between report categories would not result due to differences in the physical presentation parameters, we randomly extracted as many trials from each report category as there were for the least reported category. Only these trials were forwarded to the neural analyses and all other trials were discarded. Since this extraction was performed separately for each block, the number of trials that were associated with a specific ISI (and mask size) was kept constant over all report categories. Take for example the results of one block in the metacontrast masking task whose 48 OPC trials are made up of 20 *simultaneous*, 10 *segregated* and 18 *only mask* reports. Since *segregated* reports would make up the lowest trial number, 10 trials would be randomly extracted from each report category for this block. Further participants needed to be excluded after the last recording session of each paradigm if less than 75 trials per report category could be extracted from all blocks combined (before trial exclusion). After trial exclusion, we could include for each participant between 70 and 173 trials (*M* = 100.4, *SD* = 29.1) for the metacontrast masking task, between 100 and 184 trials (*M* = 150.1, *SD* = 22.0) for the missing element task and between 66 and 180 trials for the two-flash task (*M* = 143, *SD* = 26.4).

2.6.1 Behavioral data analysis

Since similar (temporal) processes might be relevant in metacontrast masking, the missing element and two-flash task, we investigated the relationship between their behavioral results. A popular parameter in the two-flash task is the fusion threshold, a measure of the temporal resolution of our visual system, which is reflected in the ISI that marks the transition of discriminating one flash from two flashes (Reeves, 1996; Samaha & Postle, 2015). The fusion threshold may hence mark that ISI in which a temporal integration or segregation of the stimulus presentation is equally likely. Accordingly, we defined the fusion threshold in both the missing element and the two-flash task as being reflected in the ISI with a correct report proportion of 50%. For the metacontrast masking task we defined the fusion threshold as that ISI in which report proportions of *simultaneous* and *segregated* percepts intersected. We determined fusion thresholds based on all data of the recording sessions of each paradigm. Eventually, we performed Spearman's rank correlations between the fusion thresholds of each paradigm and corrected for multiple testing using the FDR method (Benjamini & Hochberg, 1995). Since the temporal resolution of our visual system should equally affect the fusion threshold in each of our paradigms, we expected to find a positive correlation and hence conducted one-sided tests. Participants were excluded pairwise from these correlations if we could not compute their respective fusion thresholds. This was the case in the metacontrast masking task if the report proportions of *simultaneous* and *segregated* reports did not intersect ($n = 1$) and in the missing element ($n = 0$) and two-flash task ($n = 4$) if the proportions of correct reports always stayed under or above 50%.

2.6.2 Electrophysiological data analysis

All electrophysiological data were recorded with a *Biosemi Active Two* system with 64 scalp electrodes. Electrodes were placed according to the 10-20 system and their offsets were kept at a maximum of ± 20 mV. Additional electrodes were placed on the outer canti of both eyes, under the left eye and on both mastoids. Online, data were recorded with a sampling frequency of 1024 Hz. Offline, data were down-sampled to 512 Hz and re-referenced to the average of both mastoid electrodes. All preprocessing and analyses were performed in *MATLAB* (*The Math Works, Inc.*, Version R2013b) using custom-build code and the *EEGLAB* toolbox (Delorme & Makeig, 2004). We applied a bandpass filter between 0.1 and 100 Hz (IIR Butterworth filter, 12 dB/octave) and epoched the data into trials from -1000 to 1000 ms around the onset of the first stimulus in each task. Only trials with an OPC presentation were kept for further analysis. Large motor artefacts were discarded by visual inspection. Afterwards, ocular artefacts were corrected using an independent component analysis (Jung et al., 2000) that was separately applied to each task and recording session. Trials with remaining artefacts and ocular artefacts around target onset (-200 to 400 ms) were discarded from the dataset by visual inspection. On average, we discarded between 1.4 and 19.0% of all trials for the metacontrast masking task (*M* = 6.5%, *SD* = 4.9%), between 0.5% and 22.7% of all trials for the missing element task (*M* = 6.9%, *SD* = 6.1%) and between 0.3% and 22.4% of all trials for the two-flash task (*M* = 6.5%, *SD* = 5.9%). For the two-flash task, we changed the electrode positions so that electrodes over the right hemisphere were always contralateral to the flash presentation.

For each task, we analyzed the event-related potentials (ERP) in the time window between -200 and 1000 ms around the onset of the first stimulus. A baseline correction was applied by subtracting the average activity in the pre-stimulus time window from each trial. Our ERP analysis followed a component-oriented approach. If possible, we defined the spatiotemporal distribution of each ERP component by inspecting the average ERP irrespective of reports. This resulted in slightly different definitions for each ERP component for each task (table 1): This method was not applicable to the VAN and the CIN since they already represent ERP differences. Thus, we defined their spatiotemporal distributions based on previous findings in the literature. The CIN was defined in accordance with findings from the metacontrast masking (Kraut & Albrecht, 2022) and the missing element task (Akyürek et al., 2010) that both showed a centralized topography 200 to 450 ms after stimulus onset. The VAN was defined in accordance with its typical appearance in the N1-N2 time window and occipito-temporal electrodes (Railo et al., 2011). To check for ERP differences between report categories, we inserted their averaged spatiotemporal ERP values into a repeated measures ANOVA. This was done separately for each ERP component and task. By adding an additional spatial factor to each ANOVA, we explored the spatial distribution for each ERP difference. While early ERP components (P1, N1, N2, VAN) were investigated for differences in their lateralized distribution, later ERP components (CIN, early P3, late P3) were investigated for differences in their fronto-occipital distribution.

**** Insert table 1 here ****

3. Results

3.1 Behavioral results

Over the course of the ISI in the metacontrast masking task, we found the report proportions of the *simultaneous* percept to decrease while that of the *segregated* percept increased (figure 3a). Additionally, report proportions of the *only mask* percept showed an inversed U-shaped function over the course of the ISI. Linear and quadratic trends were significant for the courses of report proportions of each percept (all $p < .001$). The average OPC for each participant was made up of an ISI ranging between 13.67 ms and 75 ms ($M = 34.53$ ms, $SD = 14.70$ ms) and a mask size ranging between 1.97° (2.44 pixels contour size) and 2.86° (15 pixels contour size; $M = 2.42°$ (8.77 pixels contour size), $SD = 0.28°$ (3.87 pixels contour size)). The stability of the ISI and mask size of the OPC between recording sessions was assessed by spearman's rank correlations which indicated a high retest reliability for both the ISI ($r(22) = .96$, $p < .001$) and mask size ($r(22) = .95$, $p < .001$). The fusion threshold ranged between 11 ms and 61 ms ($M = 31.91$, $SD = 12.76$).

**** Insert figure 3 here ****

Over the course of the ISI in the missing element task, we found the proportion of correct reports to decrease (figure 3b). Both the linear and quadratic trends were significant for the course of correct report proportions (all $p < .001$). Thus, the identification of the missing element became more difficult, the more time passed between the presentation of each grid. The average OPC for each participant was made up of an ISI ranging between 12.50 ms and 40.63 ms (*M* = 27.89 ms, *SD* = 8.31 ms) and the fusion threshold ranged between 14 ms and 56 ms (*M* = 30.48 ms, *SD* = 9.41 ms).

Over the course of the ISI in the two-flash task, we found the proportion of correct reports to increase for both the evaluation of one flash and the evaluation of two flashes (figure 3c). The performance of evaluating two flashes showed a significant linear and quadratic trend (all $p < .002$) over the course of the ISI and the performance of evaluating one flash differed significantly between the shortest (*M* = .89, *SD* = .10) and longest (*M* = .97, *SD* = .04) ISI ($t(21) = -4.360$, $p < .001$). In addition, the proportion of reporting two flashes in the lowest ISI was higher for the presentation of two flashes (*M* = .31, *SD* = .21) compared to the presentation of one flash (*M* = .14, *SD* = .14; $t(22) = -5.086$, $p < .001$). In sum, discriminating two flashes from each other became easier the more time passed between the two flashes and participants tended to rely on both the evaluation of the sequence of events and the evaluation of the overall stimulus presentation duration. The average OPC for each participant entailed an ISI ranging between 8.59 ms and 55.47 ms (*M* = 31.05 ms, *SD* = 11.50 ms). The fusion threshold ranged between 19 and 48 ms (*M* = 29.58, *SD* = 8.34).

Spearman's rank correlation between the fusion thresholds of each paradigm (figure 3d) resulted in a high correlation between the metacontrast masking and the missing element task ($r(20) = .51$, $p = .023$). No correlation could be found between the fusion thresholds of the two-flash and both the missing element ($r(17) = .02$, $p = .474$) and the metacontrast masking task ($r(17) = .25$, $p = .209$).

3.2 Electrophysiological results

A summary of our inferential ERP results can be found in table 2. A descriptive visualization of the ERP results is depicted in figure 4 for the metacontrast masking task, in figure 5 for the missing element task and in figure 6 for the two-flash task.

**** Insert table 2 here ****

**** Insert figure 4 to figure 6 here ****

For the comparison of *simultaneous* to *only mask* reports in the metacontrast masking task, we found marginally significant differences in the N1 and significant differences in the VAN and early P3. Differences in the N1 showed a marginally significant main effect ($F(1,23) = 3.582$, $p = .071$) depicting more negative amplitudes for *simultaneous* (-1.50 µV) than *only mask* reports (-1.06 µV). Differences in the VAN showed a significant main effect ($F(1,23) = 4.847$, $p = .038$) depicting more negative amplitudes for *simultaneous* (-1.04 µV) than *only mask* reports (-0.61 µV). Differences in the early P3 showed a significant interaction effect ($F(2,46) = 4.030$, $p = .024$) depicting more pronounced positive amplitudes for *simultaneous* than *only mask* reports in electrodes of the left (4.81 µV compared to 4.53 µV) and right hemisphere (5.75 µV compared to 5.49 µV) but not in the center (4.98 µV compared to 5.06 µV).

For the comparison of *segregated* to *only mask* reports in the metacontrast masking task, we found marginally significant differences in the VAN, and significant differences in the CIN and early P3. Differences in the VAN showed a marginally significant interaction effect (*F*(1,23) = 4.754, *p* = .040) depicting more pronounced negative amplitudes for *segregated* than *only mask* reports in electrodes in the center (0.10 µV compared to 0.71 µV) than in the left (-1.36 µV compared to -1.07 µV) or right hemisphere (-1.82 µV compared to -1.46 µV). Differences in the CIN showed a significant main effect (*F*(1,23) = 7.749, *p* = .011) depicting more negative amplitudes for *only mask* (4.02 µV) than *segregated* reports (4.66 µV). Differences in the early P3 showed both a significant main (*F*(1,23) = 5.901, *p* = .023) and interaction effect (*F*(2,46) = 3.910, *p* = .027) depicting more negative amplitudes for *only mask* (5.03 µV) than *segregated* reports (5.67 µV) which was more pronounced in electrodes of the left (4.53 µV compared to 5.38 µV) and right hemisphere (5.49 µV compared to 6.15 µV) than in the center (5.06 µV compared to 5.48 µV).

For the comparison of *simultaneous* to *segregated* reports in the metacontrast masking task, we found marginally significant differences in the early P3 and significant differences in the N2 and CIN. Differences in the N2 showed a significant main effect (*F*(1,23) = 4.754, *p* = .040) depicting more negative amplitudes for *simultaneous* (2.43 µV) than *segregated* reports (2.94 µV). Differences in the CIN also showed a significant main effect (*F*(1,23) = 4.544, *p* = .044) depicting more negative amplitudes for *simultaneous* (4.19 µV) than *segregated* reports (4.66 µV). Differences in the early P3 showed a marginally significant main effect (*F*(1,23) = 3.895, *p* = .061) depicting more negative amplitudes for *simultaneous* (5.18 µV) than *segregated* reports (5.67 µV).

For the missing element task, we found a marginally significant effect for the

N1 and a significant effect for the late P3. Differences in the N1 showed a marginally significant interaction effect (*F*(1,21) = 3.808, *p* = .065) depicting more pronounced negative amplitudes for correct than incorrect reports in electrodes of the right hemisphere (-5.61 µV compared to -5.21 µV) compared to electrodes in the left hemisphere (-3.15 µV compared to -3.02 µV). Differences in the late P3 showed a significant main effect (*F*(1,21) = 7.331, *p* = .013) depicting more positive amplitudes for correct (5.76 µV) than incorrect reports (5.24 µV).

For the two-flash task, we found a significant effect for the P1. Differences in the P1 showed a significant interaction effect (*F*(1,21) = 8.036, *p* = .010) depicting more positive amplitudes for correct (1.44 µV) than incorrect reports (1.13 µV) in ipsilateral electrodes and more negative amplitudes for correct (0.68 µV) than incorrect reports (0.94 µV) in contralateral electrodes.

4. Discussion

In this study, we concurrently investigated the neural correlates of temporal and masking mechanisms in a metacontrast masking task by comparing the electrophysiological activity of temporally integrated, temporally segregated and masked percepts against each other. Moreover, we assessed the degree of shared processes in paradigms that investigate temporal mechanisms by additionally investigating the neural correlates in a missing element task and a two-flash task by contrasting the electrophysiological activity of correct and incorrect reports against each other. For the metacontrast masking task, we demonstrated the visual awareness negativity and late positivity for a comparison of either the temporally integrated or segregated percept against the masked percept. Moreover, we found the contour integration negativity for a comparison of either the temporally integrated or masked percept against the segregated percept. For the missing element task, we found a late P3 effect indicating a more positive amplitude for a successful temporal integration. For the two-flash task, we found a P1 effect indicating more negative amplitudes for a successful temporal segregation. There was hardly any ERP evidence that indicated shared processes in any of the paradigms but a marginally significant N1 effect for both the metacontrast masking and missing element task. In addition, only the behavioral data of the metacontrast masking and missing element task showed a significant relationship with each other.

4.1 Metacontrast masking

Our behavioral data replicate our previous results (Kraut & Albrecht, 2022; Kraut et al., 2022) and show that the likelihood of reporting a temporally integrated percept was maximal for the shortest ISI and decreased the longer the ISI became. In contrast, temporally segregated reports depicted the opposite pattern and showed that the likelihood of reporting them was maximal for the longest ISI and decreased the shorter the ISI became. In addition, the likelihood of reporting a masked percept was maximal for medium ISI and decreased the longer or shorter the ISI became. These results are in accordance with previous metacontrast studies that investigated the phenomenal perception of the target-mask sequence (Reeves, 1982; Koster et al., 2020) or hypothesized the relevance of temporal processes for the masking phenomenon (Francis & Cho, 2008; Sackur, 2013; Albrecht & Mattler, 2016). Although our behavioral data alone do not implicate any relationship between temporal and masking mechanisms, they are in accordance with Reeves' (1982) dual process theory, according to which masking should result if both temporal integration and segregation fail at the same time. Thus, reports of masked percepts are most likely for medium ISI since the likelihood of a simultaneous failure of both processes is maximal here.

Our ERP results demonstrated a more negative ERP amplitude for temporally integrated than segregated reports for a broad range of occipital to central electrodes around 200 to 450 ms after target onset thereby replicating our findings in previous studies (Kraut & Albrecht, 2022; Kraut et al., 2022). Since this ERP difference closely resembles the contour integration negativity (Pitts & Martinez, 2014), it might indicate a greater engagement of contour integration processes with a temporally integrated percept. Compared to a temporally segregated percept, a temporally integrated percept depicts a larger amount of simultaneously represented contours since the target appears inside of the mask and also generates a small white gap in between of both stimuli. Interestingly, we also found a contour integration negativity for the comparison of masked with temporally segregated percepts but not with temporally integrated percepts. This indicates that the same process is equally active in the generation of temporally integrated and masked percepts. By assuming that this process reflects contour integration, our findings would indicate that masking is associated with the spatial integration of the target's and mask's contours.

In the framework of the *Boundary Contour and Feature Contour Systems* (BCS/FCS; Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994) it has been proposed that the processing of the target's contour needs to be finished before the target's surface can be filled in (Breitmeyer & Jacob, 2012). Accordingly, contour processing would not only precede surface processing but would also be a prerequisite for surface processing to take place.

A disruption of the target's contour processing would hence also disrupt the target's surface processing which would in turn reduce the target's overall visibility. Consistent with the BCS/FCS, the processing of the target's contour was proposed to be affected by two factors that compete against each other: (1) the excitatory feedback activity of the target and (2) the mask's lateral inhibition (Francis, 1997). In light of this approach, the association of the masked percept with a contour integration negativity may indicate that the mask's lateral inhibition is especially potent if the contours of both stimuli are spatially integrated. Thus, a spatial integration of the target and mask would not protect the target from masking but render the target especially susceptible to it. The maximum likelihood of a masked percept to occur in medium SOA may be due to the mask's most potent inhibitory influence on the target's contours whose neural representation already started to erode (Francis, 1997).

Since the temporally integrated percept was also associated with a contour integration negativity, its target would have also been exposed to an especially potent lateral inhibition of the mask. However, the target might have remained visible due to an increased excitatory feedback signal that the target itself generated (Francis, 1997). This might be indicated by a significant visual awareness negativity that we could demonstrate for both temporally integrated and segregated percepts compared to the masked percept. In both comparisons the visible target elicited a more negative amplitude in occipitotemporal electrodes in the N1-N2 time window. The visual awareness negativity was proposed to reflect reverberating feedback activity within the ventral stream (Railo et al., 2011) and may hence reflect the intensity of the target's excitatory feedback activity in the BCS/FCS (Francis, 1997).

Consistent with the visual awareness negativity that is usually followed by a late positivity we also demonstrated more positive amplitudes for the temporally integrated and segregated percept compared to the masked percept in parietal electrodes 300 to 450 ms after target onset. Both the visual awareness negativity and the late positivity have been demonstrated in metacontrast masking with performance-based tasks by comparing trials in which the target shape was correctly or incorrectly identified (Railo & Koivisto, 2009). Although the identification of target contours seems to be related to its visibility, there may be other processes that affect the processing of the target contours while preserving the visibility of the target. Due to this uncertainty of the participating processes, it is debated which neural correlates genuinely reflect the awareness of the target and which reflect sensory or post-perceptual processes (Railo et al., 2011). Our study complements previous research that used performance-based tasks by utilizing a purely phenomenal task that allowed a comparison of the reported awareness and unawareness of the target. Since we replicated the visual awareness negativity and late positivity, our study supports their interpretation as reflecting crucial processes that affect the visibility of a visual object.

Eventually, although our findings can be explained in light of the BCS/FCS, they contradict Reeves' (1982) dual process theory. In this theory, a concurrent failure of both temporal integration and segregation would result in masking. Thus, all processes that would be associated with either temporal integration or segregation should not be present when masking occurs. This assumption is violated since the contour integration negativity was associated with both the temporally integrated and masked percept. Additionally, the visual awareness negativity may indicate the relevance of target processing for the masking effect which is hardly consistent with the approach of the dual process theory that tries to explain the masking effect solely on the ground of temporal processing.

4.2 Missing element task

Participant’s ability to detect the missing element tumbled from 88% correct identifications in the lowest ISI when both grids directly followed each other to 15% correct identifications in the longest ISI of 75 ms. This core finding of the missing element task (Hogebn & Di Lollo, 1974; Di Lollo, Hogben, & Dixon, 1994; Akyürek et al., 2010; Sharp et al., 2019; Wutz et al., 2016) indicates that the more time passes between both grid presentations the less likely or worse their temporal integration becomes which in return lowers the likelihood of correctly identifying the missing element. Interestingly, the fusion thresholds of both the missing element and metacontrast masking task significantly correlated with each other thereby indicating that the same processes may partake in both tasks.

By comparing correct and incorrect trials in the missing element task, we found an effect on the late P3 depicting more positive amplitudes for correct trials in parietal electrodes from 450 to 750 ms after target onset. This effect replicates previous findings in the missing element task that also demonstrated more positive amplitudes for the late P3 (Akyürek et al., 2010). The authors of this study interpreted this finding as reflecting a decreased effort to consolidate the representation of one integrated representation (correct report) compared to two separate representations (incorrect report) in working memory. This interpretation is in line with findings demonstrating a steady reduction in the P3 amplitude with an increasing number of elements that needed to be kept in visual memory (Vogel & Machizawa, 2004).

Previous findings also indicated an N2 and early P3 effect that resulted from more negative amplitudes for correct reports (Akyürek et al., 2010). The authors interpreted this effect as an increased effort of a spatial integration process which would fit the contour integration negativity that shows a large spatiotemporal overlap with these components. Although we could find effects in the N2, early P3 and the contour integration negativity for the comparison of temporally integrated and segregated percepts in the metacontrast masking task, we found neither effect for our missing element task. This discrepancy to previous findings in the missing element task may have resulted from differences in the presentation parameters. In our study, both grids were presented for 12.5 ms and they were separated from each other by an average ISI of 27.89 ms. In comparison, Akyürek et al. (2010) presented their first grid for 70 ms, their second grid for 10 ms and separated them from each other by an ISI of 10 ms. It is especially conceivable that a reduced ISI may have contributed to an increased spatial integration of both grids in the study by Akyürek et al. (2010).

In addition, we found a marginally significant effect on the N1 showing more negative amplitudes for correct trials in parieto-occipital electrodes of the right hemisphere from 150 to 190 ms after target onset. This effect also replicates previous findings in the missing element task that demonstrated more negative amplitudes for correct trials in the N1 (Akyürek et al., 2010). The authors of this study interpreted this N1 effect either as reflecting feature integration or a consequence of a previously successful temporal integration. According to our results, this N1 effect may also reflect a masking effect. Although correct trials in the missing element task can be attributed to a successful temporal integration of the stimulus sequence, incorrect trials may result from a variety of processes, e.g. from a successful temporal segregation of the stimulus sequence or from the second grid masking the first. Thus, ERP differences in the N1 may also reflect a comparison of temporal integration and masking processes. This interpretation is especially imposing since we found the very same effect for the metacontrast masking task exclusively for a comparison of temporally integrated and masked percepts. The possibility of masking processes being present in the missing element task has been hypothesized before (Akyürek & Wijnja, 2018; Kraut & Albrecht, 2022). Moreover, since no other ERP correlate is shared by the missing element and metacontrast masking task, masking may explain the relationship between their fusion thresholds. However, since the N1 effects of both of our tasks are only marginally significant, their association with masking should be taken with caution.

4.3 Two-flash task

Participant's performance in correctly identifying the presentation of two successive flashes increased from an average of 31% correct identifications for the shortest ISI of 19 ms to an average of 94% correct identifications for the longest ISI of 75 ms. This pattern of results may either result from an evaluation of perceiving one or two events or an evaluation of the overall presentation duration of the stimuli. According to our data, participants used both strategies since (1) the presentation of one flash was also erroneously reported as two flashes when its presentation duration was short and (2) the presentation of two flashes was still reported more often when two flashes were presented compared to when only one flash was presented. Therefore, a comparison of correct and incorrect trials for our two-flash task might not purely reflect a comparison of successful and failed temporal segregations but also differences in mechanisms that time stimulus durations.

By comparing correct and incorrect trials in the two-flash task, we found an effect on the P1 depicting more negative amplitudes for correct trials in occipito-parietal electrodes of the contralateral hemisphere and more positive amplitudes for correct trials in the occipito-parietal electrodes of the ipsilateral hemisphere. This effect may reflect a differential deployment of spatial attention to either visual hemifield since the sequence of two flashes could unpredictably occur in the periphery of the left or right visual hemifield. Consistent with this interpretation, the P1 has been demonstrated to be more positive when attention has been deployed on the location of stimulus presentation (Hillyard, & Anllo-Vento, 1998). However, according to our results a more positive P1 and hence an enhanced deployment of attention to the location of the flash presentation would reduce task performance. Although this seems counter-intuitive at first, an increased spatial attention has been demonstrated to lower participant's temporal resolution in the two-flash task (Yeshurun & Levy, 2003). Thus, our P1 effect is in line with a differential deployment of spatial attention in the two-flash task and supports a detrimental effect of spatial attention on the temporal resolution of our visual system.

Apart from this P1 effect, we did not find any other significant ERP difference. A previous ERP study that investigated the two-flash task demonstrated no P1 effect but a N1 effect that depicted a more negative amplitude for trials with a successful temporal segregation (Ronconi et al., 2017). However, a more negative N1 amplitude has not only been demonstrated for successful temporal segregations in the two-flash task but also for successful temporal integrations in the missing element task both in the literature (Akyürek et al., 2010) and in our study.

This renders the N1 effect debatable to reflect temporal processing and renders it more likely to reflect another aspect of stimulus processing.

4.4 Limitations and future research

A minor limitation for interpreting the results of the two-flash task is that participants not only evaluated the sequence of events but also the total stimulus presentation duration. Therefore, we cannot be sure whether a correct identification of two flashes as a sequence of events is due to a successful temporal segregation or a process that times stimulus presentation durations. This second process could only be detected since we also implemented catch trials in which only one flash was presented. Another study that also implemented trials with the presentation of only one flash, did not report such an effect (Samaha & Postle, 2015). However, in this study each individual flash was presented far longer (40 ms) than in our study (12.5 ms) and hence the impact of the ISI on the total stimulus presentation duration was less. Thus, the short target durations of our study might have increased the attractiveness to rely on a strategy to rate the overall stimulus presentation duration. We would recommend future studies to also implement catch trials to determine the strategies that participants use to solve the two-flash task.

We needed to exclude half of our participants in the course of the metacontrast masking task since the spectrum of parameters that we adapted to create an optimal presentation condition did not work for all of our participants. This exclusion rate may seem high at first sight. However, we wanted participants to report three different percepts to the same degree despite we were presenting them with the same stimulus presentation over and over again. Against this background, we rate an exclusion rate of only 50% as a success. In the literature, there are quite some parameters like the target-mask distance (Cox, Dember, & Sherrick, 1969), the mask duration (Breitmeyer, 1969) or the mask size (Kao & Dember, 1973) that apart from the variation of ISI depict a relationship with the proportion of masked reports. Although these results may give the impression that varying the proportion of masked reports is an easy task, these results constitute in most cases participant averages that do not necessarily generalize in the exact same way to the individual level. Our own piloting data indicated that a variation of the mask size while keeping the target-mask distance constant worked best to linearly variate the masking proportion on an individual level.

4.5 Conclusion

By concurrently investigating the neural correlates of temporal and masking mechanisms in a metacontrast masking task, we demonstrated that both temporal integration and masking are associated with a contour integration process. This shared processing characteristic is hardly to be aligned with the dual process theory of metacontrast (Reeves, 1982) but can be explained in the framework of the boundary contour and feature contour systems (Grossberg & Mingolla, 1985; Grossberg & Mingolla, 1988; Grossberg, 1994; Francis, 1997; Breitmeyer & Jacob, 2012). In addition, just like previous studies on metacontrast masking that used a performance-based task, our phenomenal task produced a VAN and LP for the comparison of masked and unmasked trials. This finding not only further validates our phenomenal approach but also supports the interpretation of the VAN and LP as neural correlates of visual awareness.

To assess the degree of shared processes in paradigms that investigate temporal mechanisms, we also determined the neural correlates of temporal integration and segregation in a missing element and two-flash task. Neither behavioral nor neural data of the two-flash task showed any relation or overlap with the metacontrast masking or missing element task. In contrast, there might be a shared process for the missing element and metacontrast masking task since their behavioral data are positively related with each other. Whether or not this process constitutes a masking process, like it is indicated by a marginally significant N1 effect for both paradigms, remains speculative.

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Figure Captions

Figure 1. Depiction of average report proportions for temporally integrated, temporally segregated and masked percepts in a metacontrast masking task. Parameters of the mask size were systematically varied and its influence on report proportions investigated. Each line corresponds to one session in which one parameter of the mask size was kept constant while the other two mask size parameters were manipulated. Overall, six participants participated in this piloting study. In each session, 756 trials were presented and equally distributed to each SOA and mask size variation. Each data point in the graph is hence based on 42 trials. MT = mask thickness, MEL = mask edge length, TMD = target-mask distance.

Figure 2. Depiction of the stimuli (left) and procedure (right) for each paradigm. All ISI were presented equally often in the training session of each paradigm. In the EEG sessions, the optimal ISI was presented in 50% of all trials and was adapted before each block to ensure that *simultaneous* and *segregated* reports were made equally often. (a) In the metacontrast masking paradigm, not only the optimal ISI but also the mask size was varied before each block to ensure that *only mask* reports were made as often as *simultaneous* and *segregated* reports. (b) In the missing element task, participants were requested to equally disperse their attention inside of a fixation field. (c) In the two-flash task, flashes were presented either to the left or right of the fixation. In each trial, flashes were presented on the same side of the fixation. In catch trials, the flash was also presented in the ISI thereby converting the sequence of two flashes into one continuous flash.

Figure 3. Depiction of the behavioral data results for each task. (a) Report proportions for each percept in the metacontrast masking task as a function of the inter-stimulus interval. Report proportions in each inter-stimulus interval add up to one. (b) Report proportions of correctly reporting the missing element in the missing element task as a function of the inter-stimulus interval. (c) Report proportions of correctly reporting one flash when one flash was presented and two flashes when two flashes were presented as a function of the inter-stimulus interval. In cases of one flash the flash was also presented in the inter-stimulus interval. (d) Correlations between the fusion thresholds (FT) of each task. The fusion threshold was defined separately for each participant and task as the inter-stimulus interval in which (1) report proportions of *simultaneous* and *segregated* percepts intersected for the metacontrast masking task, (2) proportions of correct reports showed a performance of 50% in the missing element task or (3) proportions of correct two-flash reports showed a performance of 50% in the two-flash task.

Figure 4. Depiction of the participant average ERP for the metacontrast masking task. **(upper part)** Depiction of ERP curves separately for each report category and a selected sample of representative electrodes. Shaded areas depict time intervals and electrodes that were used to calculate ERP components. **(lower part)** Depiction of topographies for the average ERP and ERP differences between report categories. Each topography represents the average of a 50 ms time interval.

Figure 5. Depiction of the participant average ERP for the missing element task. **(upper part)** Depiction of ERP curves separately for correct and incorrect reports and a selected sample of representative electrodes. Shaded areas depict time intervals and electrodes that were used to calculate ERP components. **(lower part)** Depiction of topographies for the average ERP and ERP differences between correct and incorrect reports. Each topography represents the average of a 50 ms time interval.

Figure 6. Depiction of the participant average ERP for the two-flash task. **(upper part)** Depiction of ERP curves separately for correct and incorrect reports and a selected sample of representative electrodes. Shaded areas depict time intervals and electrodes that were used to calculate ERP components. **(lower part)** Depiction of topographies for the average ERP and ERP differences between correct and incorrect reports. Each topography represents the average of a 50 ms time interval.

Figures

Figure 1

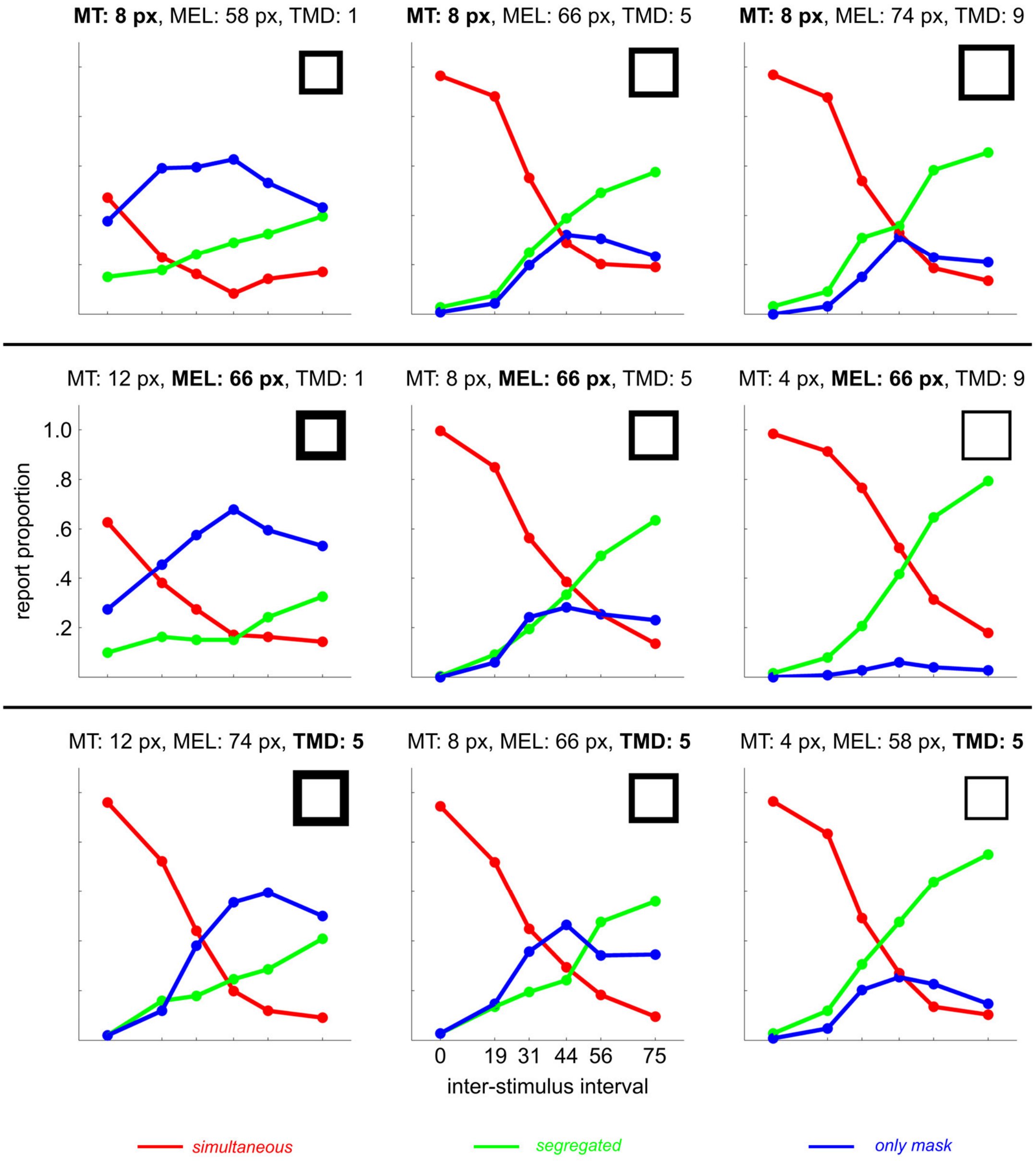
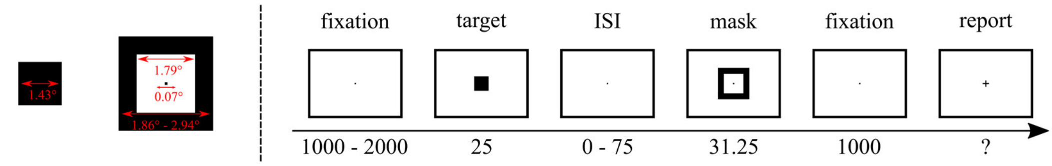
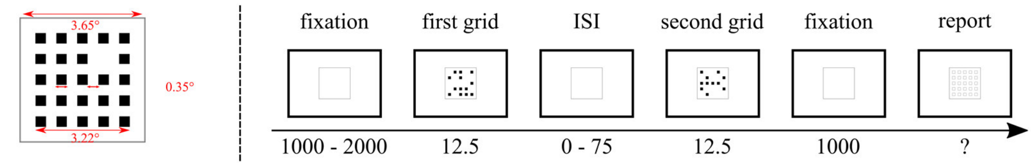


Figure 2

(a) metacontrast masking



(b) missing element task



(c) two-flash task

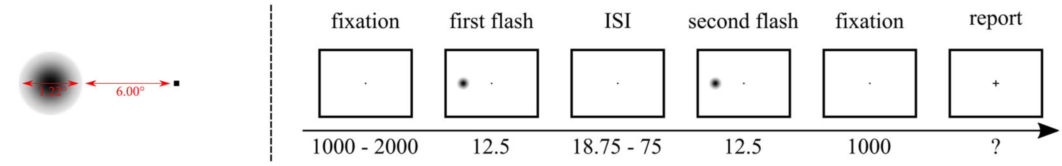


Figure 3

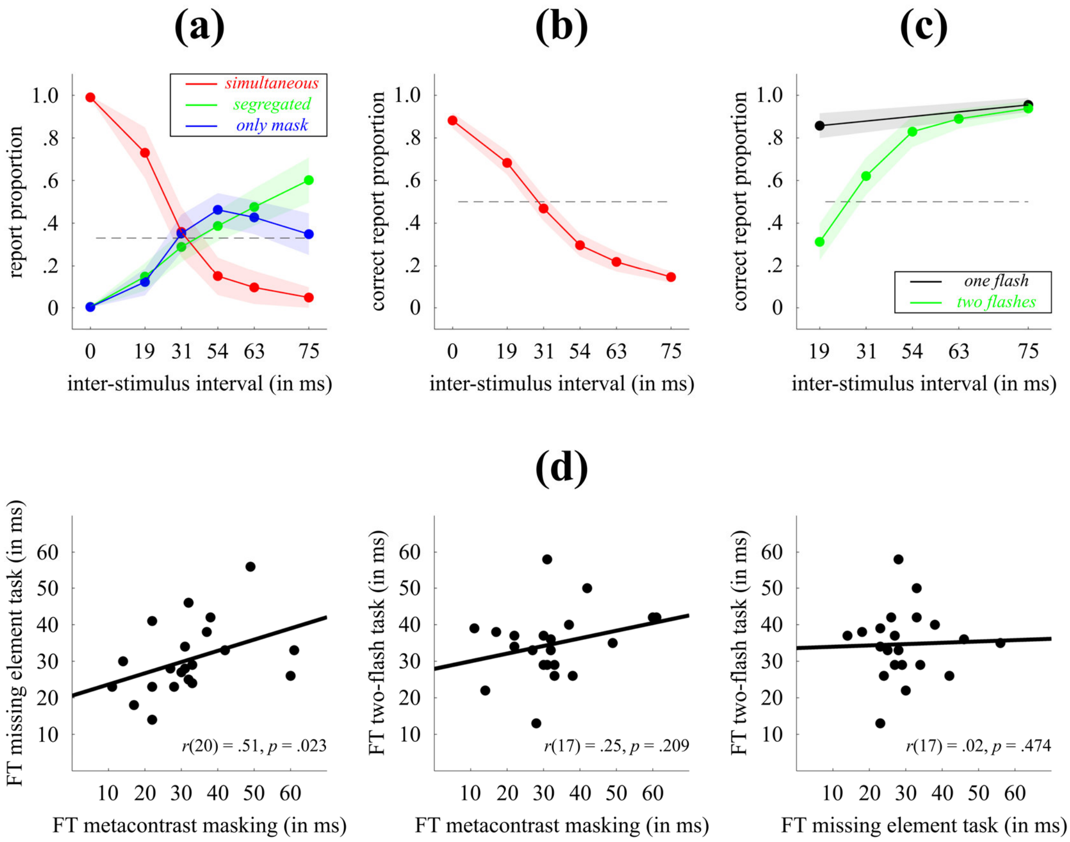

(a)
(b)
(c)
report proportion
1.0
.8
.6
.4
.2
0
simultaneous
segregated
only mask
0
19
31
54
63
75
inter-stimulus interval (in ms)
correct report proportion
inter-stimulus interval (in ms)
correct report proportion
one flash
two flashes
inter-stimulus interval (in ms)
(d)
FT missing element task (in ms)
60
50
40
30
20
10
r(20) = .51, p = .023
FT metacontrast masking (in ms)
FT two-flash task (in ms)
r(17) = .25, p = .209
FT metacontrast masking (in ms)
FT two-flash task (in ms)
r(17) = .02, p = .474
FT missing element task (in ms)

Figure 4

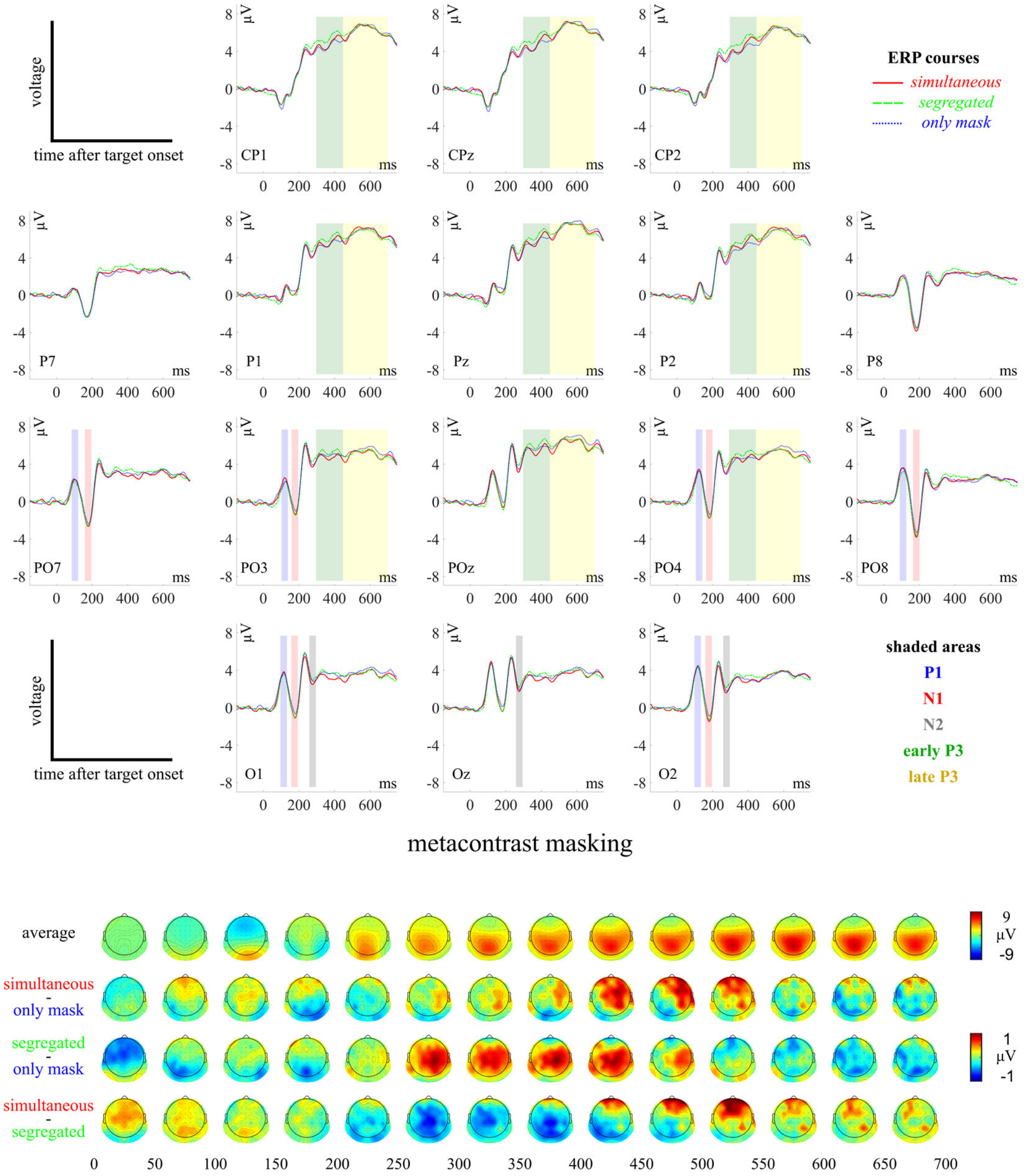
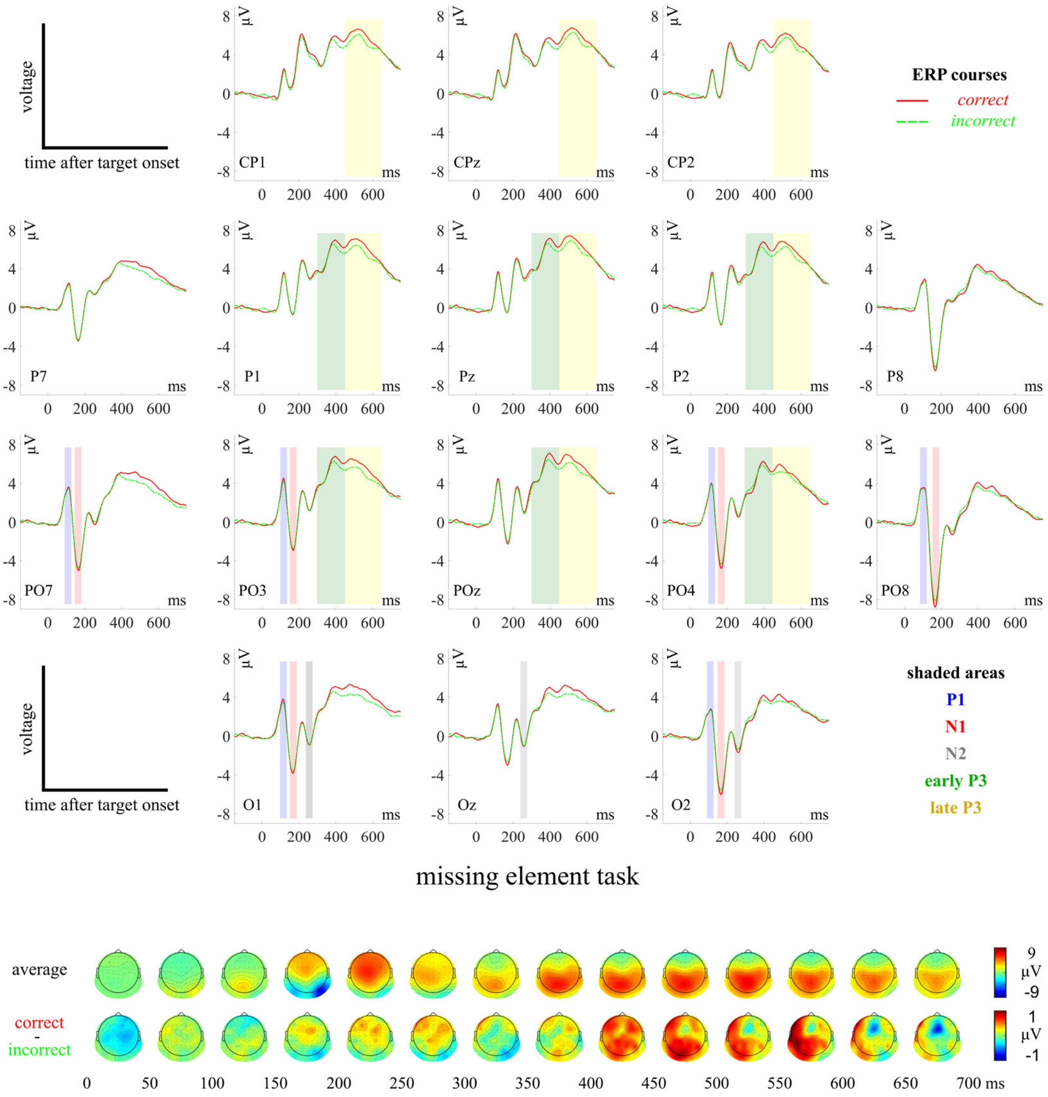

voltage
time after target onset
8
4
0
-4
-8
µV
ms
0 200 400 600
CP1
CPz
CP2
P7
P1
Pz
P2
P8
PO7
PO3
POz
PO4
PO8
O1
Oz
O2
ERP courses
simultaneous
segregated
only mask
shaded areas
P1
N1
N2
early P3
late P3
metacontrast masking
average
simultaneous - only mask
segregated - only mask
simultaneous - segregated
9
µV
-9
1
µV
-1
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700

Figure 5


voltage
time after target onset
CP1
CPz
CP2
ERP courses
correct
incorrect
P7
P1
Pz
P2
P8
PO7
PO3
POz
PO4
PO8
O1
Oz
O2
μV
ms
8
4
0
-4
-8
0
200
400
600
shaded areas
P1
N1
N2
early P3
late P3
missing element task
average
correct
-
incorrect
9
μV
-9
1
μV
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50
100
150
200
250
300
350
400
450
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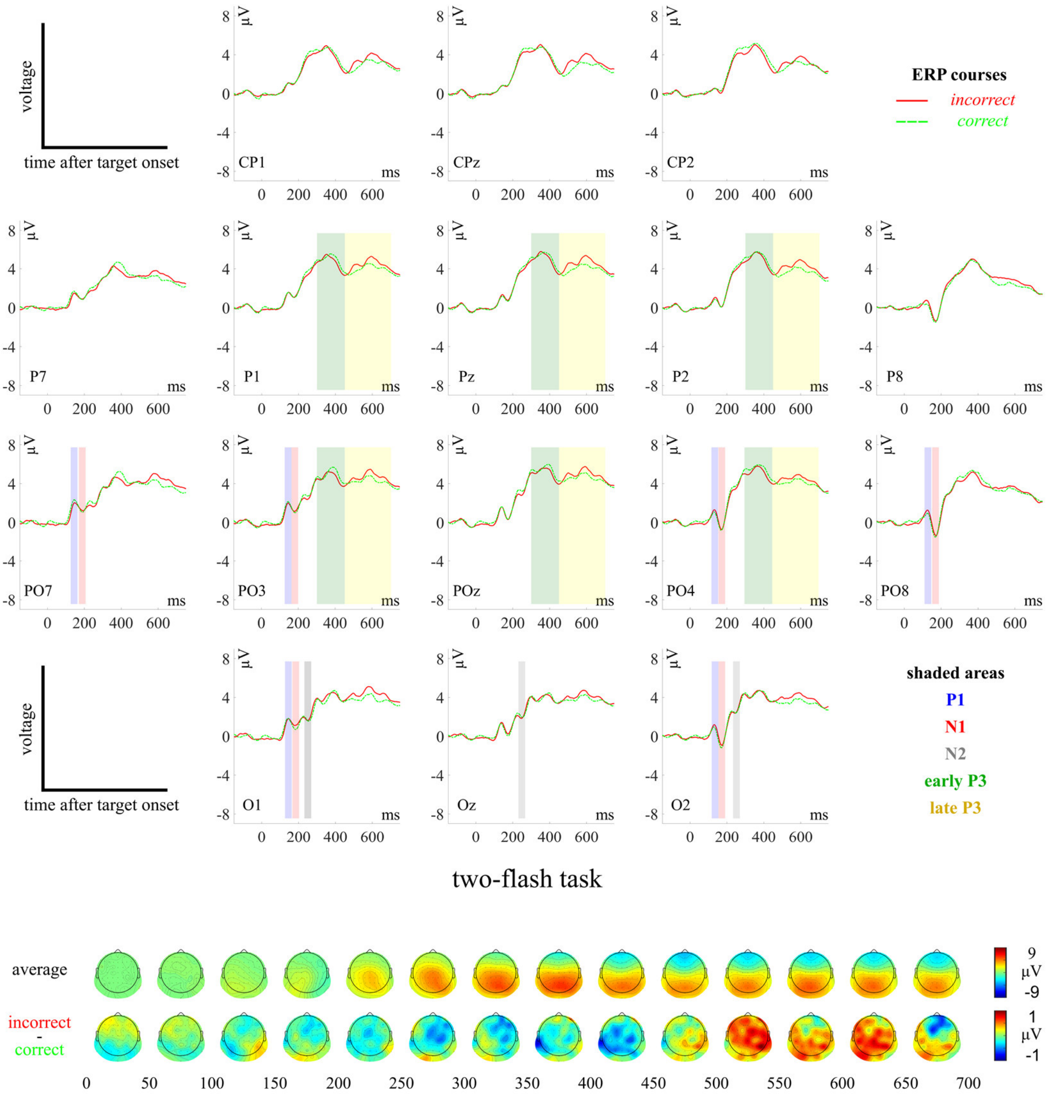
550
600
650
700 ms

Figure 6


voltage
time after target onset
CP1
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ERP courses
incorrect
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shaded areas
P1
N1
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early P3
late P3
two-flash task
average
incorrect
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700

Table 1

Definition of the spatiotemporal distribution of each ERP component separetely for each task

Component	Time			Channels		
	MCM	MET	TFT	MCM	MET	TFT
P1	90 - 130 ms	90 - 130 ms	110 - 150 ms	left: PO7, PO3, O1 right: PO8, PO4, O2		
N1	160 - 200 ms	150 - 190 ms	150 - 190 ms	left: PO7, PO3, O1 right: PO8, PO4, O2		
N2	250 - 290 ms	230 - 270 ms	230 - 270 ms	left: O1 center: Oz right: O2		
VAN	150 - 200 ms			left: P5, P7, PO7, PO3, O1 center: POz, Oz right: P6, P8, PO8, PO4, O2		
CIN	200 - 450 ms			frontal: C1, Cz, C2 center: CP1, CPz, CP2 occipital: P1, Pz, P2		
early P3	300 - 450 ms			frontal: CP1, CPz, CP2 center: P1, Pz, P2 occipital: PO3, Poz, PO4	frontal: P1, Pz, P2 occipital: PO3, POz, PO4	frontal: P1, Pz, P2 occipital: PO3, POz, PO4
late P3	450 - 750 ms			frontal: CP1, CPz, CP2 center: P1, Pz, P2 occipital: PO3, Poz, PO4	frontal: CP1, CPz, CP2 center: P1, Pz, P2 occipital: PO3, Poz, PO4	frontal: P1, Pz, P2 occipital: PO3, POz, PO4

Note. Electrodes are grouped according to the levels of the spatial factor that was inserted into the repeated-measures ANOVA to explore the spatial distribution of each ERP difference.

MCM = metacontrast masking task, MET = missing element task, TFT = two-flash task

Table 2

F values for the repeated-measures ANOVA that was performed separately for each ERP component, task and comparison of report categories.

Component	Effect	MCM (*n* = 24)			MET (*n* = 22)	TFT (*n* = 24)
		simultaneous - only mask	segregated - only mask	simultaneous - segregated	correct - incorrect	incorrect - correct
P1	report	0.26	0.99	1.94	0.19	0.02
	report * lateralization	0.22	.13	0.04	0.73	**8.04**
N1	report	*3.58*	1.76	0.13	2.16	0.46
	report * lateralization	0.78	0.01	1.19	*3.81*	0.10
N2	report	1.25	0.36	**4.75**	0.19	0.01
	report * lateralization	0.73	0.93	0.54	1.55	0.20
VAN	report	**4.85**	2.81	0.01	0.81	0.20
	report * lateralization	0.97	*2.96*	1.91	1.77	0.10
CIN	report	0.38	**7.75**	**4.54**	1.83	1.83
	report * frontal/occipital	0.36	1.01	1.11	0.57	0.57
early P3	report	0.32	**5.90**	*3.90*	1.63	1.07
	report * frontal/occipital	**4.03**	**3.91**	0.80	0.34	1.02
late P3	report	0.23	0.25	0.01	**7.33**	2.79
	report * frontal/occipital	2.23	1.85	1.31	0.04	1.93

Note. F values are reported for both the main effect of the report category (report) and the interaction effect between the report category and the spatial distribution of the ERP difference (lateralization or frontal/occipital). Bold *F* values depict significant effects ($p < .05$) while italic *F* values depict marginally significant effects ($p < .1$). Moreover, blue shades depict at least marginally significant negative differences while red shades depict at least marginally significant positive differences.

MCM = metacontrast masking task, MET = missing element task, TFT = two-flash task

Supplementary information

for the manuscript

Neural correlates of temporal and masking processes: a concurrent investigation in a multi-paradigm study

by

Alexander T. A. Kraut and Thorsten Albrecht

It contains the following sections:

1. Time-frequency analysis of phase and power data

1.1 Introduction

Differences in temporal processing have repeatedly been associated with pre-stimulus phase differences, for example in the missing element task (Wutz, Muschter, Koningsbruggen, Weisz, & Melcher, 2016; VanRullen, 2016a), the two-flash task (Varela, Torro, John, & Schwartz, 1981; Milton & Pleydell-Pearce, 2016; Ronconi, Oosterhof, Bonmassar, & Melcher, 2017) and the metacontrast masking task (Kraut & Albrecht, 2022; Kraut, Sandberg, & Albrecht, 2022). To explain this finding, most theories propose a periodic variation of the neural excitability due to neural oscillations to be fundamental for temporal processing (Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Jensen, Gips, Bergmann, & Bonnefond, 2014). Accordingly, it was suggested that (1) temporal integration windows form around the most excitable phase of an oscillation's cycle (Varela et al., 1981), (2) temporal representations are impaired when the lag of a stimulus sequence coincides with the least excitable phase of an oscillation's cycle (Milton & Pleydell-Pearce, 2016) or (3) the perceived lag between a sequence of two stimuli depends on how fast each stimulus is processed and eventually exceeds a perceptual threshold (VanRullen, 2016a).

Especially lower frequency bands like the theta (Hanslmayr et al., 2013) and alpha frequency band (Jensen et al., 2014) have been demonstrated to periodically vary the neural excitability due to their potentially high amplitude. Although this would translate into the hypothesis that phase and power effects on temporal processing should interact, neither such an interaction nor a main effect of power has been demonstrated for lower frequency bands (Milton & Pleydell-Pearce, 2016). An absence of these effects runs counter to the idea that phase effects on temporal processing reflect a periodic variation of the neural excitability. Milton and Pleydell-Pearce (2016) hence propose that phase effects on temporal processing are independent from power effects and reflect a fundamental periodicity in the neural information transfer between brain areas, for example the thalamocortical dialog.

Such an approach would also be more in line with findings that not only lower neural frequencies but also higher neural frequencies like the beta frequency band depict a phase effect on temporal processing (Fujioka, Trainer, Large & Ross, 2012; Arnal, Doelling & Poeppel, 2015; Baumgarten, Schnitzler, & Lange, 2015; Kraut & Albrecht, 2022; Kraut et al., 2022). Although their lower amplitudes limit their potential to periodically vary the neural excitability, they may also reflect a fundamental information transfer in the neural system that affects temporal processing. Apart from phase differences, an increased pre-stimulus beta power has been associated with an increased likelihood for a successful temporal integration (Geerligs & Akyürek, 2012; Wutz, Weisz, Braun, & Melcher, 2014). This effect has been termed the “integration readiness” (Geerligs & Akyürek, 2012) and was associated with the degree of attentional deployment and participant’s anticipation of the upcoming stimulus presentation which both might affect temporal processing despite not reflecting temporal processing itself.

Pre-stimulus phase differences have not only been demonstrated to affect temporal but also consciousness phenomena. The reported awareness of stimuli that are presented at detection threshold was demonstrated to be dependent on the theta and alpha phase that they are presented in (Busch, Dubois, & VanRullen, 2009). Moreover, the trough compared to the hill of an alpha cycle has been associated with an increased detection rate of the target in a metacontrast masking task (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Both studies associated their phase effects to reflect a periodic variation in the neural excitability that affects the processing of stimuli. In line with this approach, Mathewson et al. (2009) demonstrated their alpha phase dependence only for trials with a high alpha power. This runs counter to the phase dependence of temporal phenomena in which no such interaction between phase and power effects has been demonstrated. Thus, although both temporal and consciousness phenomena show a phase dependence in lower neural frequencies, their mechanisms may differ.

We already investigated the neural correlates of temporal integration and segregation in metacontrast masking in two previous studies, in which we compared the neural activity of trials with a temporally integrated and segregated report of the target-mask sequence against each other (Kraut & Albrecht, 2022; Kraut et al., 2022). In these studies, we demonstrated the presence of pre-stimulus phase differences in metacontrast masking just as they are reported in the temporal processing literature. While alpha and theta phase differences were associated with bottom-up processes, beta phase differences were associated with top-down processes. Additionally, we found no meaningful power effects on temporal processing. However, both studies lacked a concurrent investigation of both temporal and masking phenomena. Our current study is designed to extend on our previous research by comparing the neural activations of trials with a temporally integrated, segregated and masked perception of the target-mask sequence against each other. In this way, we not only further investigated the phase and power effects of temporal and masking phenomena but were also able to investigate their relationship with each other. In addition, we compared power and phase effects between paradigms to investigate whether they share any processes.

1.2 Method

Following our preprocessing routine, we calculated the event-related spectral perturbation using a continuous wavelet transform with frequencies ranging from 4 to 29 Hz in steps of 1 Hz and with time points from -680 to 0 ms before stimulus presentation in steps of 10 ms. To counter differences in the frequency precision between lower and higher frequencies, we steadily increased the cycle number for higher frequencies (4-5 Hz: 2, 6 Hz: 3, 7-9 Hz: 4, 10-12 Hz: 5, 13-19 Hz: 6, 20-29 Hz: 7). The resulting complex values were used to calculate both power and phase data (Cohen, 2014). Power data were baseline corrected relative to the average power for the whole pre-stimulus time period. To retain both absolute and phasic power differences between report categories, we used a condition-average baseline. Phases between report categories were compared by calculating the phase opposition sum (POS; see e.g. VanRullen, 2016b). The POS constitutes the summed inter-trial coherence (ITC) of each report category that was corrected for the overall inter-trial coherence irrespective of report category. Since the ITC ranges between 0 and 1, the POS ranges between 0 and 2 whereby higher POS values indicate a phase difference between report categories. Inference statistical analyses were performed for both the POS and power differences by applying non-parametric cluster-based permutation tests. To do so, we adapted the analysis procedure reported in our previous study (Kraut & Albrecht, 2022) which, however, is in fact not applicable to the analysis of the POS in our current study. Please read more on this in the discussion. The current results of our inference statistical analysis should hence be taken with extreme caution. Power and POS values were separately analyzed for each paradigm and frequency band but all electrodes and pre-stimulus time points were inserted into the analysis.

For the power, we used the analysis procedure reported in Maris and Oostenveld (2009). First, the significance of each electrode-time combination was determined by a t-test between report categories with an alpha of 5% and a two-sided test. Second, directly neighboring significant electrode-time combinations were clustered and their absolute t values summed. Cluster t sums were then compared to a distribution of cluster t sums that resulted from a null effect. This distribution resulted from assigning the power values of each participant randomly to each report category and then conducting all previously described steps. We repeated this step for 100 000 times and never used a specific assignment twice. From each of these permutations, we extracted the largest cluster t sum which as a whole constituted the null distribution. The upper 5th percentile of this null distribution was used as a threshold for cluster significance.

This approach was not applicable to the POS since it (1) already summarizes the phase states of both conditions into one value and (2) is always greater than zero, rendering the usage of t-tests inappropriate (VanRullen, 2016b). Therefore, we combined the analysis procedure reported in Maris and Oostenveld (2009) with the resampling procedure reported by Busch et al. (2009). Accordingly, we created 1000 permutations for each participant by randomly assigning the same amount of trials to each report category and then calculating the POS. Importantly, this random assignment was done separately for each block to keep physical stimulation parameters constant between report categories.

Afterwards, we drew random POS values for each participant from these permutations and calculated the participant average. By repeating this step for 100 000 times, we created a distribution of average POS values under the assumption of a null effect for each electrode-time combination. The upper 5th percentile of this null distribution was used as a significance threshold for each electrode-time combination. Directly neighboring significant electrode-time combinations were clustered and their POS values summed. Cluster POS sums were then compared to a distribution of cluster POS sums that resulted from a null effect. This distribution was generated by extracting the largest cluster POS sum from each individual dataset that make up the null distribution. The upper 5th percentile of this distribution was used as a significance threshold for each cluster.

1.3 Results

Our analyses demonstrated no significant cluster of phase differences (figure S1) but two significant clusters of power differences (figure S2). For the metacontrast masking task, we found larger power values for *simultaneous* than *segregated* reports in occipital electrodes around 400 ms before stimulus presentation. For the missing element task, we found larger power values for correct than incorrect reports in centro-parietal electrodes around 350 ms before stimulus presentation.

**** Insert figure S1 and figure s2 here ****

1.4 Discussion

Assuming that correct reports in the missing element task are associated with a successful temporal integration, both of our clusters of significant power differences would associate a larger pre-stimulus power with an increased chance of temporally integrating the later stimulus presentation. We thereby replicate previous effects that associated an increased pre-stimulus beta power with an “integration readiness” in a missing element task (Geerligs & Akyürek, 2012) and the anticipation of an upcoming sensory change in a forward masking task (Wutz et al., 2014). Interestingly, both studies depict similar topographies as we do: While both missing element tasks demonstrated a centro-parietal topography, both masking tasks demonstrated an occipital topography. Power differences have been less associated with temporal mechanisms than phase differences. At the core of many neural theories on temporal mechanisms, phase differences have been explained to reflect a periodic variation in the neural excitability. Power effects would be naturally anticipated in these theories and hypothesized to interact with phase effects: the larger the power of a neural oscillation the greater its periodic variation of the neural excitability. Main effects of power, however, are hard to fit into this framework. Thus, beta power effects have been associated with a top-down deployment of attention that optimally tunes the visual system for the upcoming stimulus presentation (Geerligs & Akyürek, 2012; Wutz et al., 2014) but not with temporal processing itself.

Both temporal (Varela et al., 1981; Milton & Pleydell-Pearce, 2016; VanRullen, 2016a) and masking effects (Mathewson et al., 2009) have been associated with a periodic variation in the neural excitability through phase states of neural oscillations (Hanslmayr et al., 2013; Jensen et al., 2014). Thus, it is essential for both the comparison of temporal and masking mechanisms as well as the assessment of shared processes between paradigms to also investigate phase effects. As a first approach to this analysis, we applied the same analysis protocols that we have already applied in our previous studies (Kraut & Albrecht, 2022; Kraut et al., 2022). However, our phase results are neither final nor even preliminary since the framework of applying inferential statistics via permutation tests has substantially changed from our previous to our current study.

While we permuted over the whole recording session in our previous studies, we are permuting separately for each block in our current study. This became necessary since physical presentation parameters could not be kept constant over the recording session anymore but differed between blocks. Compared to a full permutation, permutating separately for each block tremendously limits the variation in possible permutations and hence renders the resulting permutation datasets more similar to the unpermuted dataset. Since the combinatoric analysis behind these permutations is non-trivial, assume that we have a study with eight blocks and two trials each, one trial for each percept category and hence 16 trials total. Compared to a full permutation with 12 870 possible permutations, we would only have 256 (2^8) possible blockwise permutations; a proportion of 2%. Not only is this proportion quite low but the missing permutations would also entail those permutations with the greatest variance. A full permutation would for example entail fatigue and learning effects since an unbalanced number of trials from the first and second half of the session could be assigned to each condition. This would not be possible anymore for a blockwise permutation. Unfortunately, blockwise permutations for inferential statistics have not been described in the literature and the remaining time of the doctorate that was associated with this paper did not suffice for finding an elaborated way on our own.

Since our analyses of the phase data are not final, the absence of any phase effect should be interpreted with extreme caution. In addition, a working phase analysis procedure will allow us to also investigate interactions between phase and power effects that will shed further light on the notion that phase effects in temporal and consciousness phenomena reflect periodic variations in neural excitability.

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3. Supplemental figure captions

Figure S1. Depiction of the POS results separately for each paradigm and comparison of reports. For each frequency band, inferential statistics are summarized in a line plot that depicts for each time point the number of electrodes that show a significant phase difference. Topographies of the descriptive POS are plotted for each frequency band as averages of consecutive time windows with a length of 100 ms. No cluster reached significance.

Figure S2. Depiction of the power results separately for each paradigm and comparison of reports. For each frequency band inferential statistics are summarized in a line plot that depicts for each time point the number of electrodes that showed a significant power difference. A negative number of electrodes indicates that the subtrahend is larger than the minuend while a positive number of electrodes indicates that the minuend is larger than the subtrahend. Topographies of the descriptive power differences are plotted for each frequency band as averages of consecutive time windows with a length of 100 ms. Electrodes that were part of a significant cluster are printed in white.

4. Supplemental figures

Figure S1

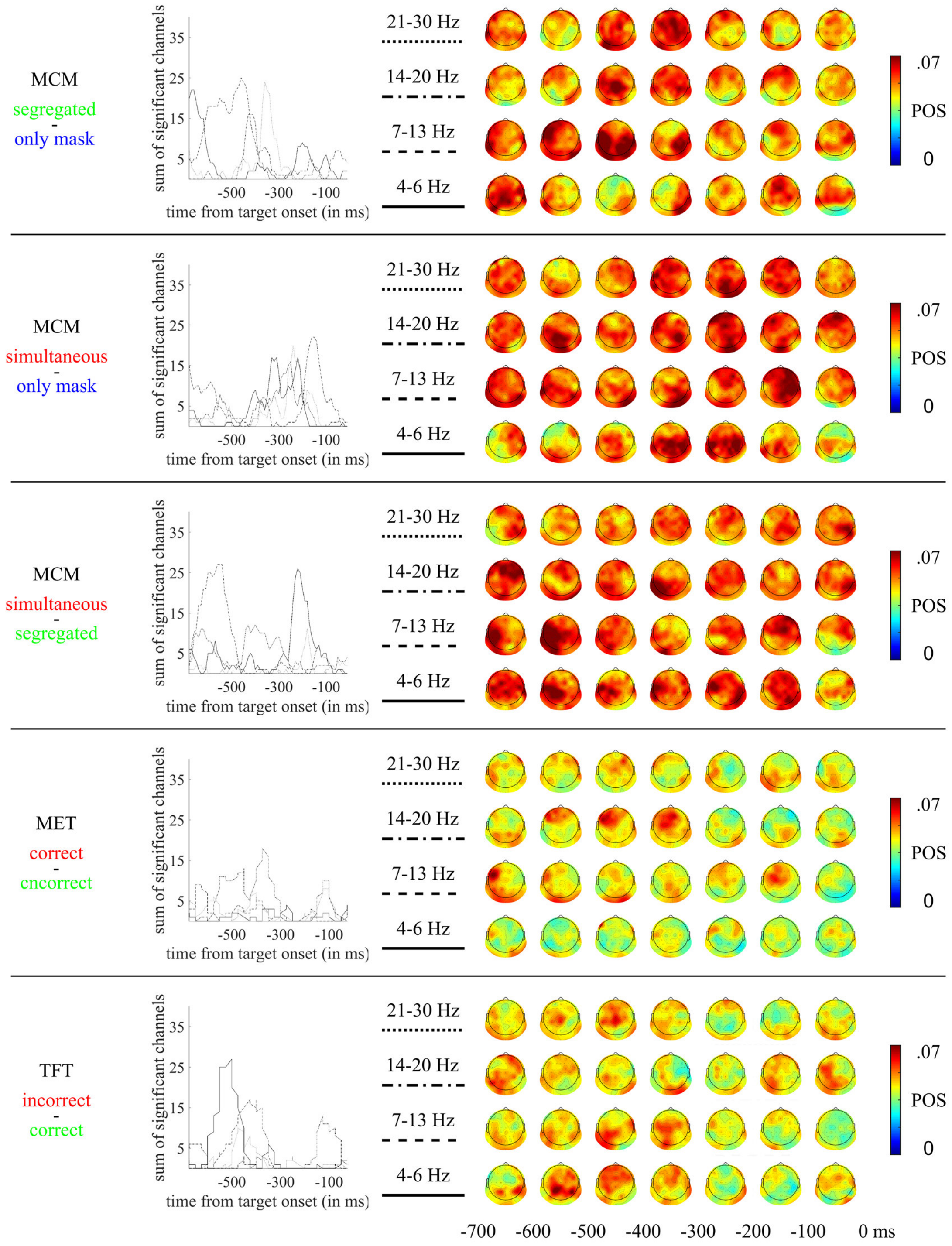
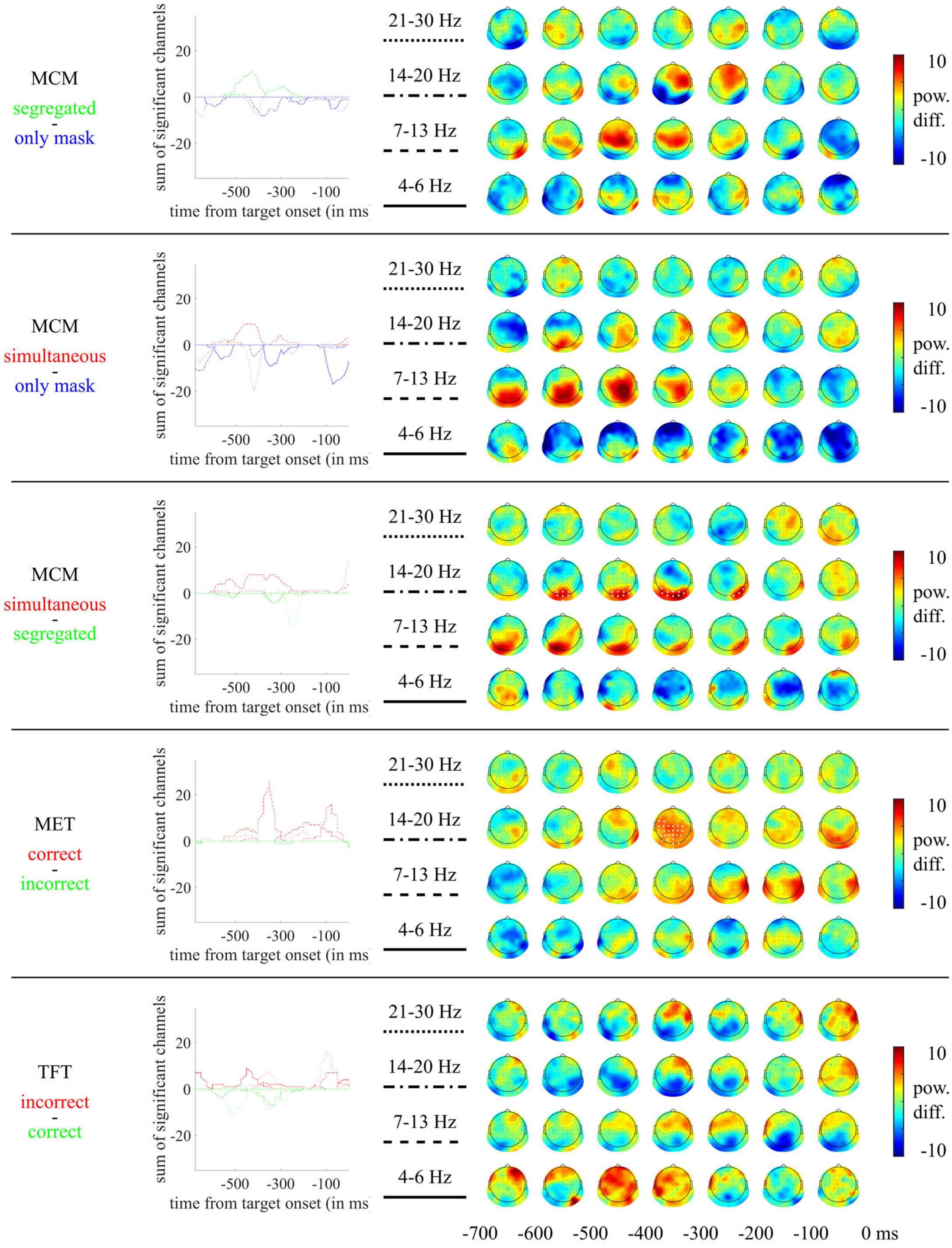


Figure S2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segregated
-
only mask
MCM
simultaneous
-
only mask
MCM
simultaneous
-
segregated
MET
correct
-
incorrect
TFT
incorrect
-
correct
sum of significant channels
20
0
-20
-500
-300
-100
time from target onset (in ms
21-30 Hz
14-20 Hz
7-13 Hz
4-6 Hz
10
pow.
diff.
-10
-700
-600
-500
-400
-300
-200
-100
0 ms