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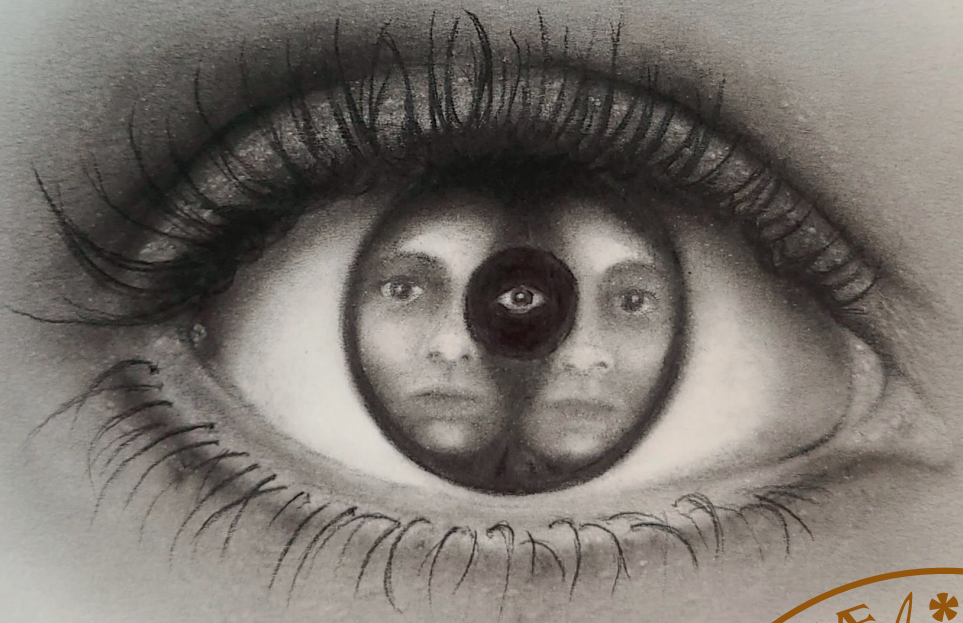
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Behavioral and Neural Aspects of Serial Dependence in Facial Identity

ANETTE LIDSTRÖM

DEPARTMENT OF PSYCHOLOGY | FACULTY OF SOCIAL SCIENCES | LUND UNIVERSITY





My primary interest is visual perceptual processes and how the brain processes the overwhelming amount of information that constantly hits our eyes. My thesis focuses on understanding the mechanisms underlying serial dependence in faces, i.e. how recently seen faces influence perceptual judgments of currently seen faces. In particular, I investigated how perceptual and working memory processing contribute to serial dependence in facial identity. My thesis contributes to understanding how perceptual and working memory mechanisms underlying serial dependence operate by actively smoothing the appearance of faces, with the specific aim of stabilizing judgments of facial identity.

Behavioral and Neural Aspects of Serial Dependence in Facial Identity

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Anette Lidström



LUND
UNIVERSITY

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Social Sciences at Lund University to be publicly defended on June 11th at 13.00 in hall Sh128, Department of Psychology, Allhelgona Kyrkogata 8, Lund

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Abstract:

The visual environment can be dynamic and often changes from one moment to the next, causing sensory input to be noisy and uncertain. In addition, internal noise from neural activity in the brain contributes to this uncertainty. Despite these challenges, the brain's visual system adeptly processes this noisy and uncertain information, creating a stable and continuous perceptual experience that allows us to navigate with a reliable sense of our environment. A phenomenon called serial dependence, in which the recent past is actively used to interpret what we are currently seeing, is thought to play a role in ensuring this perceptual stability and continuity.

Serial dependence occurs when current stimulus judgments are systematically drawn towards recent stimulus history, so that a current stimulus is judged to be more similar to a previous stimulus than it actually is. Serial dependence is known to occur for a variety of objects and features, including facial identity. Although serial dependence results in a misjudgment, it is thought to be beneficial and have a positive impact on facial recognition. The aim of my thesis was to investigate how perception and working memory contribute to serial dependence in facial identity. Paper I investigated the time course of serial dependence in facial identity from early perception to working memory stages in the context of task-related decisions. The main findings of Paper I show that merely perceiving a previous task-irrelevant face is sufficient to induce serial dependence and support the involvement of both perceptual and working memory processes in serial dependence in facial identity. Paper I further showed that serial dependence in facial identity can be separated from serial effects arising from stimulus interactions within working memory.

In Paper II, electroencephalogram was used to investigate the relation between serial dependence and working memory capacity. Results showed that in the context of dual-task demands, individual differences in working memory capacity predict serial dependence in terms of selective suppression of task-irrelevant and selective maintenance of task-relevant information. Working memory is closely intertwined with perception. Electroencephalogram and a dual-task were also used in Paper III to investigate the interactive contribution of perception and working memory to serial dependence. The results further supported selective suppression as a mechanism contributing to serial dependence as well as mechanisms such as perceptual capacity, recollection, post-retrieval monitoring and working memory maintenance, operating in part jointly and independently on different time scales. The present thesis contributes to understanding how perceptual and working memory mechanisms underlying serial dependence operate to achieve stability and continuity by actively smoothing the appearance of faces across brief temporal delays, with the specific aim of stabilizing judgments of facial identity.

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MADE IN SWEDEN 

To my parents, for always encouraging me to be me

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Some years ago, my life changed drastically when I slipped on a patch of ice and permanently injured my shoulder, which meant that I had to completely change my career path. Although I was far from confident that I had the necessary intelligence and skills, I eventually decided to study psychology at university. Considering where I am now, I think I did alright. Today, I am simply grateful to that patch of ice that literally forced me to do what I had secretly thought of for many years: To become a scientist.

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Abstract

The visual environment can be dynamic and often changes from one moment to the next, causing sensory input to be noisy and uncertain. In addition, internal noise from neural activity in the brain contributes to this uncertainty. Despite these challenges, the brain's visual system adeptly processes this noisy and uncertain information, creating a stable and continuous perceptual experience that allows us to navigate with a reliable sense of our environment. A phenomenon called serial dependence, in which the recent past is actively used to interpret what we are currently seeing, is thought to play a role in ensuring this perceptual stability and continuity.

Serial dependence occurs when current stimulus judgments are systematically drawn towards recent stimulus history, so that a current stimulus is judged to be more similar to a previous stimulus than it actually is. Serial dependence is known to occur for a variety of objects and features, including facial identity. Although serial dependence results in a misjudgment, it is thought to be beneficial and have a positive impact on facial recognition. The aim of my thesis was to investigate how perception and working memory contribute to serial dependence in facial identity. Paper I investigated the time course of serial dependence in facial identity from early perception to working memory stages in the context of task-related decisions. The main findings of Paper I show that merely perceiving a previous task-irrelevant face is sufficient to induce serial dependence and support the involvement of both perceptual and working memory processes in serial dependence in facial identity. Paper I further show that serial dependence in facial identity can be separated from serial effects arising from stimulus interactions within working memory.

In Paper II, electroencephalogram was used to investigate the relation between serial dependence and working memory capacity. Results show that in the context of dual-task demands, individual differences in working memory capacity predict serial dependence in terms of selective suppression of task-irrelevant and selective maintenance of task-relevant information. Working memory is closely intertwined with perception. Electroencephalogram and a dual-task were also used in Paper III to investigate the interactive contribution of perception and working memory to serial dependence. The results further support selective suppression as a mechanism contributing to serial dependence as well as mechanisms such as perceptual capacity, recollection, post-retrieval monitoring and working memory maintenance, operating in part jointly and independently on different time scales.

The present thesis contributes to understanding how perceptual and working memory mechanisms underlying serial dependence operate to achieve stability and continuity by actively smoothing the appearance of faces across brief temporal delays, with the specific aim of stabilizing judgments of facial identity.

Sammanfattning

Den visuella omvärlden kan vara dynamisk och föränderlig vilket skapar otydlighet i sensorisk information. Dessutom genererar hjärnans neurala aktivitet ”brus” som bidrar till denna otydlighet. Trots dessa svårigheter kan det visuella systemet i hjärnan bearbeta denna otydliga information och skapa en kontinuerlig och stabil visuell upplevelse, vilket låter oss navigera i omvärlden med trygghet. Ett fenomen kallat ’serie beroende’, där nyligen upplevd sensorisk information används för att tolka det vi ser i nuet, tros bidra till denna stabila och kontinuerliga upplevelse.

Serie beroende uppstår när visuella bedömningar systematiskt dras mot stimuli vi nyligen sett. Ett nuvarande stimulus bedöms då vara mer likt ett tidigare sett stimulus än vad det egentligen är. Fenomenet har visat sig för olika objekt och egenskaper, inklusive ansiktsidentitet. Även om serie beroende kan leda till felbedömningar, anses det vara fördelaktigt för ansiktsigenkänning. Syftet med min avhandling var att undersöka hur visuell perception och arbetsminne bidrar till serie beroende för ansiktsidentitet. I Artikel I undersökte jag hur serie beroende för ansiktsidentitet manifesteras över tid, från det tidiga perceptuella stadiet till det senare i arbetsminnet, inom ramen för uppgiftsrelaterade bedömningar. De huvudsakliga fynden visar att enbart exponering för ett ansikte, även om det inte är relevant för uppgiften, är tillräckligt för att serie beroende ska uppstå och att både perception och arbetsminne bidrar till fenomenet. Artikel I visar också att serie beroende för ansiktsidentitet skiljer sig från serieeffekter som uppstår från stimulusinteraktioner i arbetsminnet.

I Artikel II använde jag elektroencefalogram för att undersöka relationen mellan serie beroende och arbetsminneskapacitet. Resultaten visar att vid simultana uppgifter förutsäger individuella skillnader i arbetsminneskapacitet serie beroende. Detta beror på skillnader i selektiv inhibering av uppgiftsirrelevant och selektivt upprätthållande av uppgiftsrelevant information. Arbetsminne och perception är nära kopplade. Elektroencefalogram och en simultan uppgift användes även i Artikel III för att undersöka hur interaktioner mellan perception och arbetsminne bidrar till serie beroende. Resultaten ger ytterligare stöd för att selektiv inhibering, liksom perceptuell kapacitet, minnesåterkallelse och upprätthållande av minnen, delvis tillsammans och oberoende vid olika tidpunkter under stimulusbearbetning, bidrar till serie beroende.

Denna avhandling bidrar till förståelsen för hur mekanismer relaterade till perception och arbetsminne arbetar för att skapa visuell stabilitet och kontinuitet. Detta görs genom att aktivt integrera ansiktsutseenden över korta tidsperioder via serie beroende, i syfte att stabilisera bedömningar av ansiktsidentitet.

List of papers

- I. Lidström, A. (2023). Serial dependence in facial identity perception and visual working memory. *Attention, Perception & Psychophysics*, 85, 2226-2241. <https://doi.org/10.3758/s13414-023-02799-x>
- II. Lidström, A., & Bramão, I. (2025). Working memory capacity modulates serial dependence in facial identity: Evidence from behavioral and EEG data. *Vision Research*, 227, 108542. <https://doi.org/10.1016/j.visres.2025.108542>
- III. Lidström, A., & Bramão, I. (submitted). Understanding the interaction between perception and working memory in serial dependence for facial identity: Insights from EEG.

Abbreviations

ANOVA	Analysis of variance
CFS	Continuous flash suppression
DoG	Derivative of Gaussian
EEG	Electroencephalogram
ERPs	Event-related potentials
FFA	Fusiform face area
fMRI	Functional magnetic resonance imaging
Hz	Hertz
I-MDF	Item-method directed forgetting
ISI	Interstimulus interval
ITI	Intertrial interval
NSW	Negative slow wave
OFA	Occipital face area
STS	Superior temporal sulcus
TFRs	Time-frequency representations

Introduction

“Vision, in my view, is the cause of the greatest benefit to us, inasmuch as none of the accounts now given concerning the Universe would ever have been given if men had not seen the stars or the sun or the heaven.” - Plato (428-348 CE)

Human sensory systems are of fundamental importance for the acquisition of knowledge about the external world. Historically, Aristotle (384-322 CE) attributed the greatest source of this knowledge to vision. Today we are confident that Aristotle’s assumption that the eyes transmit visual information to the heart so that this information can be perceived by the soul is not true. We are also confident that vision involves more than merely the transmission of information, but is a process of exploration, learning and creation that serves as a guide in our interactions with the environment.

The external visual environment can be dynamic and often changes from one moment to the next, causing visual input to be noisy and ambiguous. Other sources of noise and ambiguity can be due to our own eye blinks, eye, head and body movements. Ambiguity and sources of noise may also arise from viewing distance (too close or too far), time, occlusion and similarity of objects and people. In addition, these sources of noise and ambiguity are accompanied by internal noise resulting from random fluctuations within neural networks in the brain. Together, these sources of noise and ambiguity make our sensory inputs highly uncertain.

Despite the drastic change in visual input that presents itself to us when we, for example, turn our heads, we generally do not experience a sense of sudden change and wonder what just happened. In fact, we tend not to think about it at all. This is due to the remarkable ability of our brain’s visual system to successfully process the overwhelming amount of noisy and ambiguous information that constantly hits the retina of our eyes and create a stable and continuous perceptual experience. A combination of mechanisms such as visual, motor and attentional systems that recalibrate spatial orientation at each fixation are thought to underlie this illusion of perceptual stability and continuity (Bridgeman, 2010). Together, they enable the brain to create a stable and continuous perception of the world, even in the face of fluctuating or incomplete sensory input, allowing us to navigate an often dynamic and changing world with a coherent and reliable sense of our environment. More recently, it has been proposed that a phenomenon termed serial dependence, in which the recent past is actively used to interpret what we are currently seeing, is

yet another phenomenon that contributes to this stable and continuous perceptual experience (Fischer & Whitney, 2014).

Serial dependence has been shown to occur for a wide variety of objects and features, including the identity of faces (Manassi et al., 2023; Pascucci et al., 2023). Serial dependence in facial identity is said to occur when the identity of a face is judged as being more similar to a recently seen face than it actually is (Liberman et al., 2014). Although serial dependence results in a misjudgment, it is thought that this phenomenon is beneficial and has a positive impact on facial recognition (Turbett et al., 2019). The aim of my thesis was to investigate the behavioral and neural aspects of serial dependence in facial identity, specifically focusing on how perceptual and working memory processes contribute to this phenomenon.

In the following, I first provide a brief overview of how past experiences may influence perceptual judgments. I then explain the phenomenon of serial dependence, its key characteristics and functional role, and the known neurophysiological evidence regarding serial dependence effects. This leads to how serial dependence is known to manifest in facial identity judgments and the theoretical models that may explain serial dependence. This is followed by an overview of the perception and recognition of faces. I then provide an overview of processes associated with working memory, perception and attention which are relevant to my thesis. Following this, I introduce the reader to the methods used in the present thesis, including how serial dependence was assessed and analyzed, the method of electroencephalogram (EEG), event-related potentials (ERPs), and time-frequency representations (TFRs). This forms the background for the three studies in which I examined the temporal dynamics of serial dependence in facial identity in the context of task-related decisions (Paper I), the contribution of working memory processes (Paper II), and the interactive contribution of perceptual and working memory processes (Paper III) to serial dependence in facial identity.

Using the past to interpret what we see

Experiences shape how we react to the world. Evolutionary scientists have long argued that the way in which humans respond to their environment is largely determined by their past (Graffin, 2015). This reasoning also applies to perception and vision. Perceptual judgments are thought to depend not only on the immediate sensory input, but also on contextual (i.e., short-term) and structural (i.e., long-term) information over space and time (Richter & de Lange, 2019; Seriès & Seitz, 2013). The traditional view of information processing in the brain is characterized by a hierarchical structure. In the visual processing system, basic and local features are analyzed in the first stages, with the complexity of visual representations increasing ascending the hierarchy (Hubel & Wiesel, 1962). However, recent computational

perspectives suggest it unlikely that such feedforward mechanisms are sufficient to achieve flexible and invariant recognition of patterns in a complex and dynamic environment (Wyatte et al., 2014).

The functionality of the primary visual cortex has been shown to be influenced by top-down factors such as attention, expectations and interpretation of the perceptual task at hand (de Lange et al., 2018). In addition, the internal mental representations of the world that are shaped by our experiences have been shown to influence the strategies the brain uses to process visual information (Gilbert & Li, 2013). Therefore, the understanding of the significance, scope and functional variability of top-down interactions in the visual cortex has changed considerably. A consensus has now emerged in vision science that conceptualizes perception as an active process in which the brain uses past sensory information to interpret current sensory input.

The notion that perception involves inferential or generative processes is a perennial concept in academic discourse. von Helmholtz (1910, originally published in 1866) discussed the notion of unconscious inference, which he postulated as the mechanism by which visual perceptions are formed, taking into account integrated sensory information and previous experience, because the information our senses receive is often ambiguous, incomplete and discontinuous. Similarly, Gregory (1980) advocated the idea that perceptual systems formulate hypotheses about the environment based on long-term experience, which are tested against incoming sensory information. Recently, it has been shown that humans quickly and implicitly learn environmental statistics that can have a modulating influence on contextual demands in perceptual judgments (Hall et al., 2018; Chalk et al., 2010; Richter & de Lange, 2019; Spaak & de Lange, 2020; Zhou et al., 2020). Perceptual judgments of detection (Evans et al., 2011; Robson et al., 2021), speed discrimination (Overney et al., 2008), direction of motion (Ball & Sekuler, 1987), target location (Sampaio et al., 2020), visual search speed (Castelhano & Witherspoon, 2016), and shape judgments (Perez et al., 2020) have all shown to be influenced by structural experiences.

Three commonly studied phenomena in which structural experience is known to have a strong modulating influence on current perceptual judgments are the expectations that light generally comes from above (Sun & Perona, 1998), that objects and people typically move slowly or remain static (Brenner et al., 1996), and that cardinal orientations (i.e., horizontal and vertical lines) are more common than oblique orientations in the natural environment (Appelle, 1972; Girshick et al., 2011). The expectation that light normally comes from above is commonly used by humans when judging shading and depth (Croydon et al., 2017; Kobayashi et al., 2021; Pickard-Jones et al., 2020; Sun & Perona, 1998), and objects and people are typically judged to be moving more slowly than they actually are (Aguado & López-Moliner, 2019; Brenner et al., 1996; Brooks & Stone, 2006; Jogan & Stocker, 2015; Rokers et al., 2018; Rushton & Duke, 2009; Weiss et al., 2002; Welchman et al.,

2008). In addition, cardinal orientations are generally perceived with greater ease and accuracy than oblique lines (Apelle, 1972; Girshick et al., 2011). Figure 1a and b illustrate examples of two of these phenomena.

In addition to structural experiences, contextual experiences also have a strong influence on perceptual judgments. One of the first phenomena to show that past contextual sensory impressions have an influence on current perceptual judgments was termed repetition priming (Lashley, 1951). Repetition priming refers to the phenomenon where repeated exposure to the same sensory information facilitates perceptual judgments, typically manifesting as an increase in performance accuracy and a decrease in reaction time (Dzafic et al., 2016; Kristjánsson & Campana, 2010; Henson, 2003; Schacter et al., 2007; Wiggs & Martin, 1998). It is thought that repetition priming effects depend on the semantic content of information and are due to both the sharpening of object features and structural object formation in the brain depending on the familiarity of the object (Martens & Gruber, 2012). Furthermore, systematic exposure to the same sensory information is thought to generate informative expectations that are used to interpret sensory input that is identical or similar to previous sensory input. Such expectations may arise from pre-activated representations of anticipated sensory information prior to the occurrence of a stimulus (Kok et al., 2014).

Another form of temporal context effect occurs when a visual stimulus is so ambiguous that prior experience is required to enable a meaningful interpretation (Teufel et al., 2018). Two-tone black and white images are excellent examples of this, and it is also a situation in which only one view of the matching original image provides sufficient experience for a meaningful interpretation. Figure 1c illustrates an example of a two-tone black and white image and the matching original image. While a single viewing of the matching original image immediately improves recognition performance, even for original images that are not consciously processed, this is not the case for repeated viewing of the same two-tone black and white image (Chang et al., 2016; Flounders et al., 2019). Neurophysiological evidence suggests that a two-tone image and its matching original are continuously integrated shortly after stimulus onset (Flounders et al., 2019) and that top-down predictions are activated before category-specific processing in the visual cortex (Kozunov et al., 2020). Furthermore, the neural activity triggered by a two-tone image revealed after interpretation has been shown to be equivalent to the matching original image and distinct from other non-matching images (Flounders et al., 2019; González-García et al., 2018).

Contextual experience may also manifest so that current perceptual judgments are repelled by recent stimulus history. This is known as adaptation, or repulsive effects, that typically occur after prolonged exposure to a preceding stimulus or when successive stimuli are highly dissimilar (Clifford et al., 2007; Grunewald & Lankheet, 1996; Kohn, 2007). For example, a rock next to a stream is typically judged as moving upwards after prolonged viewing of the downward motion of a

waterfall (Addams, 1834). Furthermore, as illustrated in Figure 1d, vertical lines may be judged as slightly tilted rightward if they are preceded by prolonged exposure to leftward tilted lines, known as the tilt-aftereffect (Gibson & Radner, 1937; Rideaux et al., 2023). The process of visual adaptation ensures that the brain remains responsive and sensitive to changes in the visual environment. It functions by adjusting the sensitivity of receptors, neural pathways and cortical regions to the prevailing visual stimulus. In this way, visual processing is optimized so that the individual can see effectively in a wide range of lighting conditions, contrasts and motion environments (Clifford et al., 2007).

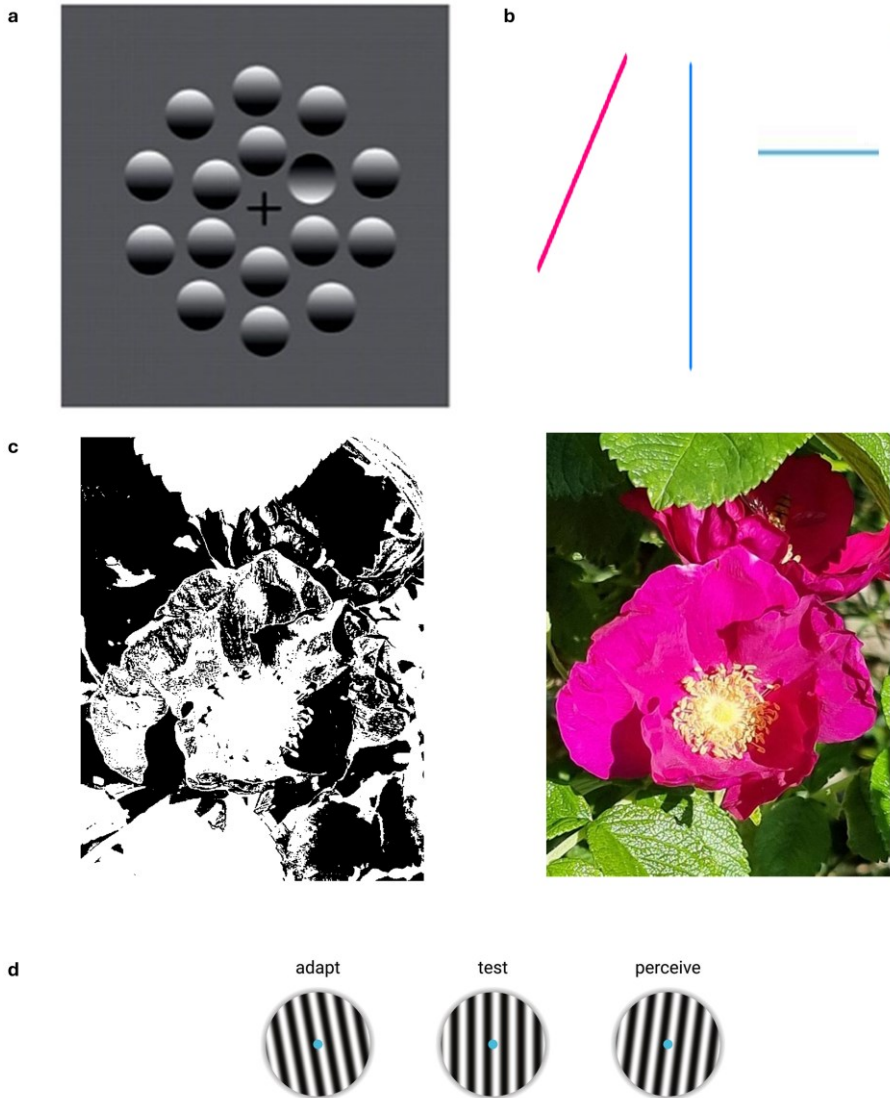


Figure 1 Prior experience in perceptual judgments

A concave shape among convex shapes is congruent with assuming that light comes from above. (b) Cardinal orientations are perceived more easily and accurately than oblique lines. (c) To interpret the two-tone black and white image to the left requires first seeing the matching original image to the right. (d) Prolonged exposure to a leftward orientation makes a subsequent test stimulus (vertical lines) look tilted in the opposite direction. Figure c is reprinted from Distinct early and late neural mechanisms regulate feature-specific sensory adaptation in the human visual system, Rideaux et al. (2023). (Copyright © 2023 the Author(s). Published in PNAS. This article is distributed under a Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0).

Humans tend to rely most strongly on prior experience when this experience is informative. Conversely, prior experience appears to have less influence on current perceptual judgments when this experience is non-informative (Mumford, 1991). As described above, prior experience can influence the interpretation of current sensory input in many ways, by improving performance accuracy and reaction time, heightening awareness and lowering recognition thresholds. Furthermore, while repeated or single exposure can generate informative expectations to resolve ambiguous sensory information, prolonged exposure to previous information may in some instances result in misjudgments. More recently, it has been suggested that brief exposure to previous stimuli can also result in misjudgments such that current perceptual judgments are drawn towards the recent past, a phenomenon termed serial dependence (Fischer & Whitney, 2014). In the following chapter, I provide a general overview of serial dependence, its key characteristics and functionality in perceptual judgments.

Serial dependence

The structured nature of sensory input from the natural environment facilitates humans' ability to learn statistical regularities (Geisler, 2008). Everyday visual tasks extend beyond the mere processing of static images, as the visual environment continuously changes over time (van Bergen & Jehee, 2019). In order to process such fluctuating sensory input effectively and accurately, the visual system needs to take account of the temporal structure between successive stimuli. To this date, significant progress is being made in understanding the mechanisms by which the visual system integrates such statistical regularities to optimize perceptual processing.

The incoming stream of sensory input is partially redundant, as the current sensory impression tends to resemble the previous one (van Bergen & Jehee, 2019). The visual system can exploit this temporal redundancy in two ways. First, it can increase efficiency by adapting to changes between successive stimuli (Weber et al., 2019), and second, it can optimize perceptual estimation by integrating recent stimulus history with the current visual input (Körding, 2007). Both ways may result in sequential effects in perceptual judgments, which can be either repulsive or assimilative. As noted in the previous chapter, repulsive effects are said to occur when a current stimulus is reported as being more different from a previously seen stimulus than it actually is (Clifford et al., 2007; Kohn, 2007). In contrast, assimilative effects are said to occur when a current stimulus is reported as being more similar to a previously seen stimulus than it actually is. Such assimilative effects have been termed serial dependence (Fischer & Whitney, 2014).

Serial dependence is said to occur when ongoing perceptual judgments are systematically drawn toward stimuli from the recent past that are no longer relevant to a current judgment. For example, when briefly viewed successive Gabor patches (i.e., sine wave gratings viewed through a Gaussian window) are presented with different orientations and the last presented Gabor patch is slightly more leftward than the current one, the current Gabor patch is typically reported to be more leftward than it actually is (Fischer & Whitney, 2014). So, when successive stimuli are similar, a previously seen stimulus appears to partially influence the judgment of a current stimulus (Manassi et al., 2023; Pascucci et al., 2023). The ubiquitous presence of serial dependence effects, now observed for stimulus dimensions such as orientation (Cicchini et al., 2018; Collins, 2019; Fischer & Whitney, 2014; Fritsche et al., 2017; Murai & Whitney, 2021; Pascucci et al., 2019), location (Bliss

et al., 2017; Fritsche & de Lange, 2019; Manassi et al., 2018; Papadimitriou et al., 2015), color (Barbosa & Compte, 2020), shape (Collins, 2022a; Manassi et al., 2019, 2021), numerosity (Cicchini et al., 2014; Corbett et al., 2011; Fornaciai & Park, 2018a; Fornaciai & Park, 2018b), ensemble perception (Collins, 2022b; Manassi et al., 2017; Pascucci et al., 2019), motion (Czoschke et al., 2019; Fischer et al., 2020), aesthetic ratings (Kim et al., 2019), age (Clifford et al., 2018; Manassi & Whitney, 2022), eye gaze (Alais et al., 2018), body size (Alexi et al., 2018) and facial attributes such as expression (Hsu & Wu, 2020; Hsu & Yang, 2013; Liberman et al., 2018; Mei et al., 2019), attractiveness (Hsu & Yang, 2013; Xia et al., 2016) and identity (Hsu & Lee, 2016; Liberman et al., 2014; Taubert et al., 2016; Turbett et al., 2019; Turbett et al., 2021), suggests that serial dependence is a fundamental property of human cognition, which is thought to contribute to a continuous and stable perceptual experience (Manassi et al., 2023). Figure 2 illustrates an overview of serial dependence for various objects and features.

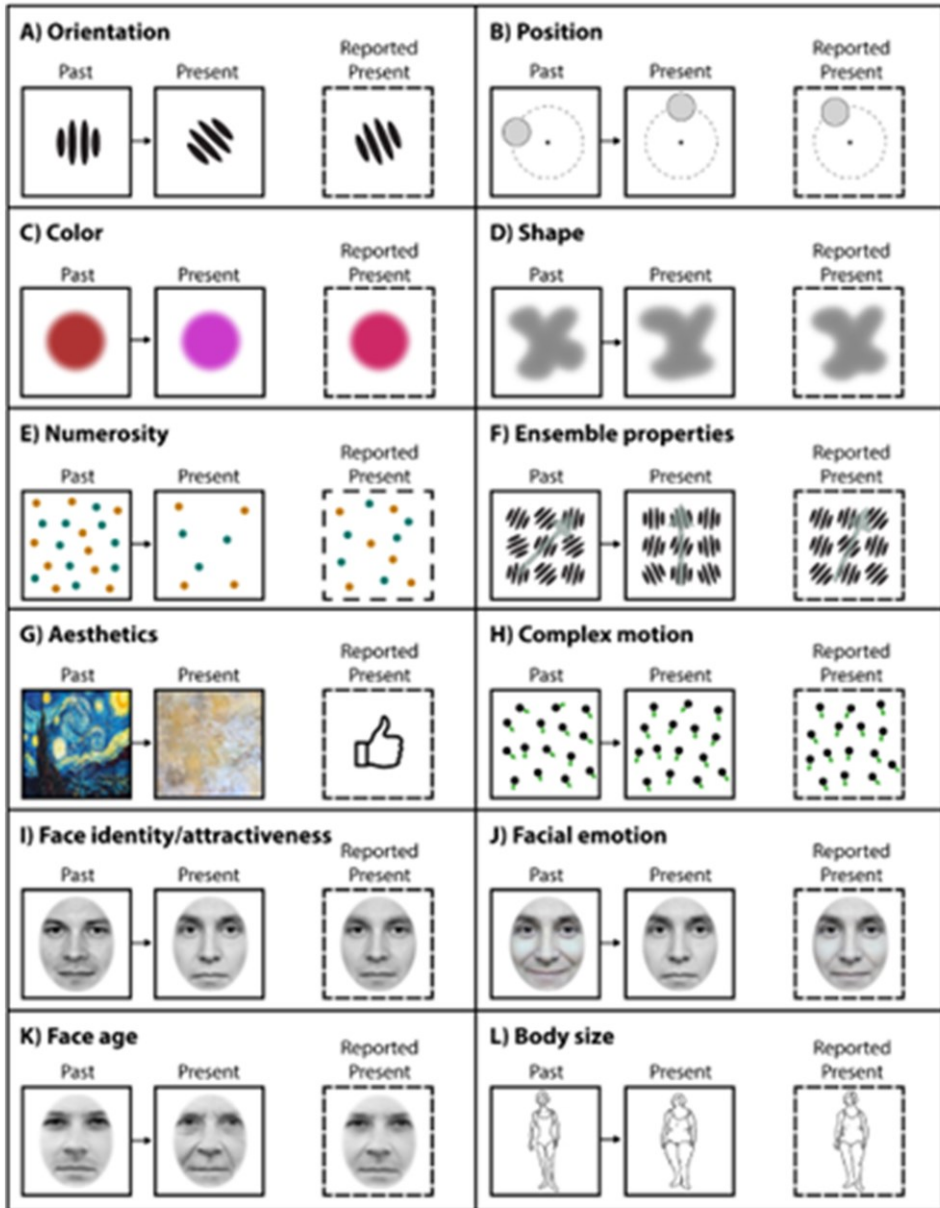


Figure 2 Serial dependence in various stimulus judgments

Past and Present refer to the previous and current stimulus respectively. Reported Present refers to the judgment of the current stimulus. Reprinted from Serial dependence in visual perception: A meta-analysis and review, Manassi et al. (2023), (Copyright © The Author(s), Published in Journal of Vision. This article is distributed under a Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0).

Key characteristics of serial dependence

Across various objects and features, four key characteristics of serial dependence have been identified. These four characteristics are: (1) temporal tuning, (2) spatial tuning, (3) feature tuning, and (4) attentional tuning. The following describes each of these characteristics and how they may play a role in perceptual judgments.

Temporal tuning

Temporal tuning refers to how the influence of past stimuli on current perceptual judgments depends on the timing of these stimuli. This means that serial dependence is most pronounced for stimuli that occurred within a certain time window relative to the current stimulus. Temporal tuning is determined by calculating the magnitude (i.e., the strength of the effect) of serial dependence across previous trials or by varying the intertrial interval (ITI) between the current and previous trial. In general, the magnitude of serial dependence decreases linearly as the time delay between the current and previous stimulus increases with an effect shown to persist ~15 s back in time (Bliss et al., 2017; Fischer & Whitney, 2014; Manassi et al., 2019; Manassi & Whitney, 2024; Papadimitrou et al., 2015). For example, Bliss et al. (2017) varied the ITI for 1, 3, 6 or 10 s and found that serial dependence in spatial position manifested most consistently for ITIs of 1, 3 and 6 s, while a repulsive effect was obtained for the 10 s ITI. Temporal tuning may help the brain to prioritize the most recent and relevant sensory information, while gradually neglecting older sensory information. However, serial dependence may, at least for orientation, depend not only on the passage of time but also on the number of intervening stimuli (Ceylan & Pascucci, 2023). In Paper I, I investigated the temporal dynamics of serial dependence over time to shed new light on the time course of serial dependence in facial identity.

Spatial tuning

Spatial tuning of serial dependence refers to how the influence of previous stimuli on current perceptual judgments depends on the spatial proximity between them. In general, the magnitude of serial dependence is stronger when successive stimuli are presented close in space and decreases as the spatial distance between stimuli increases (Cicchini et al., 2017; Collins, 2019; Fischer & Whitney, 2014; Kondo et al., 2022; Luo et al., 2022; Mikellidou et al., 2021). For example, when participants in Fischer and Whitney's (2014) study were shown oriented Gabor patches in a circular arrangement and asked to attend to and reproduce the orientation of one of them, serial dependence was obtained for orientations in the same location, while orientations in different locations showed a trend toward a repulsive effect. The visual cortex processes stimuli in a retinotopic (spatially mapped) manner, with nearby regions in the visual field represented by neighboring neurons (Fang et al., 2008). The spatial tuning of serial dependence appears to reflect this neuronal

organization, as it has been shown to be primarily retinotopic (Cicchini et al., 2017; Collins, 2019; Fischer & Whitney, 2014; Kondo et al., 2022), though other spatial reference frames (allocentric and Cartesian) may also play a role (Luo et al., 2022; Mikellidou et al., 2021). Spatial tuning could be a way for the brain to compensate for spatial inconsistencies to ensure stable perception in certain regions of the visual field.

Feature tuning

Feature tuning means that, in general, serial dependence is observed between successive stimuli that are physically similar as compared to those that are physically dissimilar (Fischer & Whitney, 2014; Liberman et al., 2014; Manassi et al., 2019; Papadimitriou et al., 2015; Pascucci et al., 2019; Turbett et al., 2021). However, feature tuning may vary depending on the experimental stimuli (Manassi & Whitney, 2024). In particular, more complex stimuli such as the variance of motion (Suárez-Pinilla et al., 2018), the attractiveness of faces (Xia et al., 2016) and the aesthetic evaluation of artworks (Kim et al., 2019) may pose a greater challenge for the manipulation of stimulus similarity than simple features such as orientation (Manassi & Whitney, 2024). Individual differences may further play a role in feature tuning, as some studies suggest that serial dependence emerges from the subjective perception of the previous stimulus rather than the physical properties of the previous stimulus *per se* (St John-Saaltink et al., 2016; Zhang & Alais, 2020). It is therefore possible that feature tuning is not adequately accounted for in the stimulus domain or in the data analysis used in some studies (Manassi & Whitney, 2024). Regardless, feature tuning may promote the brain's ability to selectively process and respond to certain features of a stimulus by recycling similar perceived or physical features.

Attentional tuning

Attentional tuning refers to how the influence of previous stimuli on judgments of a current stimulus depends on whether and how attention was directed to those stimuli. In general, serial dependence is stronger for stimuli that were actively attended to, while it weakens or is eliminated for unattended stimuli or for stimuli reported to be outside of conscious awareness (Bae & Luck, 2020; Fischer & Whitney, 2014; Fornaciai & Park, 2018b; Fu & Mei, 2024; Kim et al., 2020; Liberman et al., 2016; Rafiei et al., 2021). Fu and Mei (2024), for example, used a continuous flash suppression (CFS) technique to make the Gabor patch invisible. In CFS, one eye is presented with a static stimulus while the other eye is presented with a series of rapidly changing stimuli, resulting in suppression of the static stimulus (Tsuchiya & Koch, 2004). Participants were shown successive, randomly oriented Gabor patches, which they reproduced using an adjustment response. In one experimental condition, the Gabor patch of the previous trial was masked by a CFS stimulus. No serial dependence was obtained for masked CFS stimuli, indicating that the effect does not manifest without awareness of the stimuli.

Furthermore, feature-based attention significantly modulates serial dependence effects, as, for example, focusing on a specific attribute of a two-dimensional stimulus enhances serial dependence for this attribute as compared to the other attribute (Fritsche & de Lange, 2019). In this regard, serial dependence is amplified when successive stimuli share contextual features, such as color, highlighting the role of attentional selection to multiple features and stimuli (Fischer et al., 2020). In addition, increased sensory processing of low contrast stimuli has been shown to strengthen the serial dependence effect (Manassi et al., 2018), further emphasizing the role of attention in serial dependence. Attentional tuning may ensure that perception is selectively influenced by stimuli that are actively attended to, while unattended inputs are ignored. In Paper III, which investigated the interactive contribution of perception and working memory to serial dependence, I took advantage of the role of attention in serial dependence by superimposing a scene image of varying transparency on facial images to manipulate sensory processing and strengthen the serial dependence effect.

Continuity fields and the functional goal of serial dependence

Our sensory systems are susceptible to small fluctuations and errors. Given that objects in the external world generally remain stable over short periods of time, changes in the appearance of objects are more likely to reflect fluctuations in visual input rather than a change in the appearance of the objects themselves (Burr & Cicchini, 2014). Serial dependence tuning relates to the concept of continuity fields (Fischer & Whitney, 2014), which can be characterized as spatiotemporal regions for which stimulus judgments are systematically drawn towards immediate stimulus history (Manassi & Whitney, 2024). Continuity fields are thought to function similarly to receptive fields but with the purpose of embodying the functional goal of serial dependence, which primarily aims to stabilize perceptual judgments of noisy and dynamic sensory input (Manassi & Whitney, 2024).

In an autocorrelated visual environment, where what we are currently seeing is often a continuation of what we have recently seen, it is advantageous for the visual system to maintain a continuous attraction towards recent stimulus history to facilitate interactions within a stable context (Bayer & Zimmermann, 2023; Cicchini et al., 2014; Cicchini et al., 2018; Cicchini & Burr, 2018; Fischer & Whitney, 2014; Manassi et al., 2017; Manassi & Whitney, 2022). It has been shown that the time course of serial dependence follows the autocorrelations of emotion statistics in natural images (Ortega et al., 2023), but this is not necessarily true for basic features such as oriented Gabor patches (Blondé et al., 2023).

Serial dependence may enable faster and more accurate responses (Cicchini et al., 2018) and improve both sensitivity and confidence in contexts where current visual input is similar to visual input from the recent past (Burr & Cicchini, 2014; Cicchini & Burr, 2018; Cicchini et al., 2014; Cicchini et al., 2018; Maldonado Moscoso et al., 2023). From this perspective, adapting to temporal redundancies can be considered an efficient approach as it can lead to more reliable and accurate perceptions (Burr & Cicchini, 2014; Cicchini et al., 2018). Indeed, serial dependence has been shown to be sensitive to stimulus uncertainty (Cicchini et al., 2018; Gallagher & Benton, 2022; Kim & Alais, 2021; van Bergen & Jehee, 2019). For example, manipulating the spatial frequency or contrast of a current or previously seen oriented Gabor patch has shown that serial dependence is strongest when the spatial frequency or contrast of the current Gabor patch is low, and the previous one is high. Conversely, serial dependence is significantly reduced when the spatial frequency or contrast of a previous Gabor patch is low and the spatial frequency or contrast for a current one is high (Cicchini et al., 2018; van Bergen & Jehee, 2019). That serial dependence is modulated by stimulus uncertainty is consistent with the notion that the brain uses the temporal redundancy of the visual environment to optimize the reliability of stimulus judgments. Interestingly, using three-dimensional instead of two-dimensional oriented objects appears to strengthen the serial dependence effect, possibly due to additional stimulus uncertainty induced by the third dimension (Tanrikulu et al., 2023). Furthermore, greater confidence in current stimulus judgments is associated with weaker serial dependence (Suárez-Pinilla et al., 2018), while serial dependence is reduced when less confidence is reported for previous stimulus judgments (Samaha et al., 2019), suggesting that subjective uncertainty play a role in serial dependence.

Prioritizing stability can be useful for perceptual continuity but can also lead to errors or distortions as we are confronted with successive stimuli that are not autocorrelated when the environment changes rapidly or unpredictably (Manassi & Whitney, 2024). So, in contexts where the past is not a good predictor of the present, serial dependence can lead to suboptimal decisions and misjudgments (Cicchini et al., 2018), such as in clinical contexts and successive judgments of radiographs for different individuals (Manassi et al., 2019; Manassi et al., 2021; Ren et al., 2023a, 2023b). At the neural level, serial dependence may minimize the need for extensive neural computation over time, as the brain can reduce the computational cost of processing each new sensory input from the beginning (Cicchini & Burr, 2018; Cicchini et al., 2017; Cicchini et al., 2018).

Processing levels of serial dependence

Hitherto, the word ‘perception’ has been consistently used in relation to serial dependence in this thesis. This does not necessarily mean that serial dependence is

a purely perceptual phenomenon. Rather, it is thought that serial dependence manifests at the levels of perception, working memory and decision-making (Manassi & Whitney, 2024). Evidence for perceptual serial dependence is supported by findings showing that the physical characteristics of visual stimuli can change the appearance of subsequent stimuli, resulting in an altered perceptual experience (Cicchini et al., 2017; Collins, 2020; Fornaciai & Park, 2018a; 2018b; 2020; Goettker & Stewart, 2022; Manassi & Whitney, 2022; Murai & Whitney, 2021). For example, when participants in Manassi and Whitney (2022) watched a video showing a face that progressively became younger, the face featured at the end of the video was judged to be older than its actual age as compared to when the same face was viewed in isolation. This suggests that the preceding sequence of facial images was assimilated into the final image, resulting in a perceptual aging effect. Conversely, a video showing a progressively aging face led to the opposite result, as the face was now judged to be younger than its actual age. This experiment illustrates the continuous integration of age-related information over time, creating the illusion that the perceived age change occurred more slowly. However, whether perceptual serial dependence operates independently of higher-level cognitive functions such as working memory and decision processes is not entirely clear (Manassi & Whitney, 2024).

In addition to perception, it is thought that serial dependence manifests at higher cognitive levels, emphasizing the role of working memory (Bliss et al., 2017; Fritsche et al., 2017; Mei et al., 2019) and decision processes (Feigin et al., 2021; Fritsche et al., 2017; Pascucci et al., 2019). In this regard, serial dependence is thought to be influenced by aspects related to task performance, such as decision templates (Pascucci et al., 2019) and representations in working memory, while recent stimulus history has the opposite effect, exerting a repulsive effect away from previous stimuli. For example, Pascucci et al. (2019) showed in a series of experiments that the physical appearance of previous stimuli resulted in repulsive effects, while traces of previous stimulus decisions resulted in assimilative serial dependence. Similar results were previously shown by Fritsche et al. (2017), suggesting that serial dependence manifests post-perceptually through decision processes.

Some studies have shown that task relevance is crucial, and that serial dependence only occurs between features and stimuli that were relevant to a previous trial's task (Bae & Luck, 2020; Ceylan & Pascucci, 2023; Czoschke et al., 2019; Houborg et al., 2023a, 2023b; Pascucci et al., 2019; Pascucci & Plomp, 2021). For example, Bae and Luck (2020) conducted an experimental study in which participants were asked to focus on two-dimensional stimuli of direction of motion and color. The study included a post-cued response task in which participants reported one of the two dimensions. Results showed that serial dependence occurred only from the previously reported dimension, suggesting that the mere encoding of the unreported dimension was not sufficient to induce serial dependence. Similarly, serial

dependence is thought to operate independently of feature integration (Ceylan et al., 2021; Goettker & Stewart, 2022; Tanrikulu et al., 2023), and has been shown, for example, to manifest in orientation even though the current and previous stimuli are from different object categories (Tanrikulu et al., 2023). Furthermore, when participants were explicitly instructed to attend to the orientation of a Gabor patch during the previous trial - without providing a response - there were observable repulsive effects in the current trial that stemmed from the target orientation presented in the previous trial (Pascucci et al., 2019). In addition, in studies in which participants evaluated one of two consecutive stimuli presented within the same trial, stimulus judgments were repelled by the task-irrelevant stimulus on that trial, while simultaneously being attracted toward the task-relevant stimulus on the previous trial (Czoschke et al., 2019; Pascucci et al., 2019; Pascucci & Plomp, 2021).

The above suggests that higher-order decision processes monitor the continuous flow of information to determine between which information it is advantageous to integrate. It has therefore been argued that serial dependence reflects an active mechanism in which only relevant prior decisions exert an influence on ongoing perceptual judgments (Feigin et al., 2021). Indeed, several studies have reported serial dependence effects from the previous response, rather than the previous stimulus (Blondé et al., 2023; Gallagher & Benton, 2024; Moon & Kwon, 2022; Morimoto & Makioka, 2022; Sadil et al., 2024; Zhou et al., 2024). However, serial dependence has been shown to manifest even when there is no explicit response made to a previous stimulus, at least for judgments of numerosity (i.e., a stimulus consisting of many units or parts, Fornaciai & Park, 2018a), which suggests that in certain contexts this phenomenon may occur independently of decision processes. Numerosity is a complex stimulus which engages multiple cognitive and perceptual processes in the brain (Harvey, 2016). This observation is of particular relevance to Paper I in which I tested whether serial dependence in facial identity, which we will later learn, is also a complex stimulus that engages specialized neural circuitry, occurred in the absence of a response to a previous face.

There is also evidence that serial dependence is modulated during the maintenance of working memory. Studies have shown that the magnitude of serial dependence increases with longer temporal delays between a target stimulus and a response, suggesting that the memory representation of orientation, spatial position and facial expression shifts towards a previous stimulus over time (Bliss et al., 2017; Fritsche et al., 2017; Mei et al., 2019). In addition, Markov et al. (2024) investigated the role of working memory processes in orientation serial dependence using a dual-task experiment. Their results showed that working memory load had a significant influence on serial dependence depending on whether the target orientation on the current or previous trial was processed at high concurrent working memory load. When high working memory load was imposed on the previous trial, the magnitude of serial dependence was weaker, whereas working memory load imposed on the

current trial resulted in stronger serial dependence effects. This suggests that the maintenance of information in working memory may have an impact on the perception or memory representation of a current stimulus, leading to a shift towards a previous stimulus. Yet, serial dependence does not appear to be related to working memory capacity (Bansal et al., 2023; Zhang & Whitney, 2017), and the exact contribution of working memory processes to serial dependence remains unclear. Papers I, II, and III aimed to shed light on the relationship between serial dependence in facial identity and working memory processes. Particularly, the temporal dynamics of serial dependence during the maintenance of a current face in working memory and precisely whether task demands mediate the relationship between serial dependence and working memory processes.

Neurophysiological evidence of serial dependence

The investigation of the neural correlates of serial dependence suggests that the mechanisms underlying serial dependence may involve a variety of processing levels. Functional magnetic resonance imaging (fMRI) results have shown that for orientation, a neural signal of serial dependence can be observed in the primary visual cortex (St. John-Saaltink et al., 2016; van Bergen & Jehee, 2019), which is consistent with serial dependence emerging at early perceptual stages. Furthermore, using classification techniques on EEG data, Fornaciai and Park (2018a) found that a neural signature of serial dependence associated with numerosity perception became apparent almost immediately after stimulus onset, supporting the notion that serial dependence influences initial perceptual processing of a current stimulus. A follow-up study by the same authors found that this neural signal persisted for up to two seconds after stimulus onset, suggesting that the altered neural representation as a result of perceptual serial dependence was maintained for a considerable period of time (Fornaciai & Park, 2020). Also using classification techniques, Ranieri et al. (2022) found that the memory trace of the reported orientation in the previous trial was mainly localized in the occipitoparietal cortex. The emergence of this memory trace reached full significance shortly after the presentation of the current orientation, consistent with serial dependence acting directly on the perception of the current stimulus. The use of classification techniques has also shown that for orientation and position, the memory representation of the stimulus of the previous trial is reactivated when the target stimulus of the current trial is presented (Bae & Luck, 2019; Barbosa et al., 2020; Stein et al., 2020) and may remain active until the current response (Bae & Luck, 2019). It is therefore difficult to determine from this evidence alone whether the influence of the previous stimulus occurs mainly at the time of perception or also at a later stage during the maintenance of the current stimulus in working memory.

EEG classification results for the target stimulus and response of the previous trial have shown different temporal profiles. Zhang and Lewis-Peacock (2024) found that during the stimulus presentation of the current orientation, the memory trace of the previous trial's orientation was stronger than that of the previous response. However, prior to the current response, the memory trace of the previous response increased above that of the previous orientation. The appearance of these differences suggests that the representation of the current orientation in working memory shifted from the originally encoded orientation at the end of the trial. This finding is supported by evidence showing that although the previous trial's stimulus appears to influence current stimulus judgments, the neural code that exerts this influence does not resemble the neural code of the previous stimulus (Luo & Collins, 2023). This may suggest that the maintenance period of a current stimulus determines the observed neural signature of the serial dependence effect.

Consistent with a higher-level origin of serial dependence, Sheehan and Serences (2022) found that response patterns in the primary visual cortex were repelled by the previous orientation, although the behavioral data showed assimilative serial dependence effects. Modelling results were consistent with repulsive effects in visual cortex due to neural adaptation at encoding, possibly to reduce redundancy, and suggested that serial dependence was due to higher level readout schemes responsible for this neural adaptation. In addition, transcranial magnetic stimulation over dorsal premotor and prefrontal brain regions has been shown to reduce serial dependence in visuo- and oculo-motor tasks (Bliss et al., 2023; de Azevedo Neto & Bartel, 2021), further suggesting that higher cognitive functions play a role in serial dependence.

Because studies use different stimuli and experimental tasks, some of which are focused on higher cognitive functions such as working memory, while others focus more on perceptual processes, it is difficult to determine the exact neural loci of serial dependence effects. Serial dependence may occur at early and late stages of stimulus processing or may be due to complex interactions between sensory and cognitive brain regions. Serial dependence may be driven by signals from high-level cognitive areas that propagate downward and interact with low-level sensory areas (Cicchini et al., 2021).

Several processing levels and mechanisms may contribute to serial dependence, but so far there is no unified agreement on their specific roles or interactions. This resonates with the multifaceted nature of serial dependence across perceptual, memory and decision processes, while revealing gaps in the understanding of whether serial dependencies at multiple levels of processing are mutually exclusive or interactive in their operation. Paper III aimed in particular to shed light on the interactive contribution between perceptual and working processes to serial dependence in facial identity by utilizing the high temporal resolution of EEG.

Serial dependence in facial identity

Serial dependence in facial identity is said to occur when a current face is reported as being more similar to a previously seen face than it actually is (Lieberman et al., 2014). It is suggested that serial dependence in facial identity reflects a high-level facial coding mechanism that operates to stabilize face perception and facial representations (Turbett et al., 2019, 2021). Indeed, it has been shown that individuals who show stronger serial dependence between highly similar faces, so-called narrow feature tuning, have better facial recognition abilities than those who show serial dependence between dissimilar faces. Furthermore, this feature tuning of serial dependence for facial identity is a predictor of facial recognition ability, independent of object recognition and adaptation effects observed in both object recognition and facial identity (Turbett et al., 2019). However, it is suggested that individual differences such as gender may play a role, as male participants tend to be more prone to exhibit narrow feature tuning as compared to female participants (Hsu & Lee, 2016). Serial dependence has also been shown to be more pronounced in super-recognizers (i.e., individuals with an exceptional ability to recognize and remember faces) as compared to control participants (Marini et al., 2024), suggesting that serial dependence contributes to and enhances their facial recognition abilities.

That serial dependence may play a particular role in the processing of faces is further supported by evidence showing that this phenomenon persists across changes in visual angle (Lieberman et al., 2014; Turbett et al., 2021) and is sensitive to face inversion (Turbett et al., 2021). For example, Turbett et al. (2021) showed participants upright and inverted faces presented separately in succession and found that serial dependence was significantly stronger between upright faces than inverted faces, independent of facial recognition abilities. Furthermore, serial dependence between similar faces was most pronounced when they were shown in upright as compared to inverted position. This suggests that serial dependence operates at the level of facial identity and possibly aims to stabilize facial representations.

Although serial dependence may be a general phenomenon in face perception and facial recognition, there is evidence that this phenomenon depends on ethnic experience (Turbett et al., 2022b). Caucasian individuals have shown more pronounced serial dependence for faces of their own ethnicity as compared to Asian faces, and stronger serial dependence for similar faces is associated with better recognition performance for faces of one's own ethnicity. This relationship does not extend to faces of other ethnicities. However, greater exposure to people of another ethnicity is associated with stronger serial dependence between more similar than dissimilar faces of that ethnicity, supporting the notion that experience shapes face perception and facial recognition (Emberson, 2017). Interestingly, no difference in serial dependence between faces of own and other ethnicities has been observed for

Asian individuals, possibly indicative of cultural differences in serial dependence (Turbett et al., 2022b).

Serial dependence in facial identity has also been shown to play a role in neurodiverse populations such as individuals with autism (Turbett et al., 2022a). Individuals with autism generally have difficulty remembering and perceiving faces and report having more problems recognizing faces than individuals without autism (Stantić et al., 2022). Yet, the magnitude of serial dependence does not differ between individuals with pronounced autistic traits and healthy individuals. However, individuals with more pronounced autistic traits show stronger serial dependence between more dissimilar as compared to similar faces, suggesting that they may have reduced perceptual specialization, which may contribute to poor facial recognition abilities. In addition, attention to detail and pattern was specifically associated with serial dependence between dissimilar faces, consistent with a detail-oriented processing style in individuals with autistic traits, potentially resulting in impaired holistic face processing which reduces sensitivity to subtle differences between faces (Turbett et al., 2022a).

Sensitivity to the finer details in faces is also strongly affected by external visual noise (Chen et al., 2015; Duchaine & Nakayama, 2006). Indeed, external visual noise has been shown to modulate serial dependence in facial identity. Kim and Alais (2021) showed participants facial identities in succession, with the previous face presented with no, low or high noise. The results showed that serial dependence manifested most consistently when the previous face was presented without noise or with high noise. In this case, serial dependence effects stemming from high-noise faces were attributed to individual differences in a “general response bias” due to unreliable sensory input, toward an internal or external decision about a previous face. Individual differences in serial dependence were less pronounced for noise-free faces, which suggests that subjective decision strategies and confidence play a role in serial dependence for facial identity (Kim & Alais, 2021). However, subjective confidence ratings were not collected in Kim and Alais (2021), which somewhat limits this conclusion.

Current evidence (Turbett et al., 2019, 2021, 2022a, 2022b) suggests that the extent to which serial dependence manifests specifically for similar faces is critical for effective facial recognition, consistent with a functional role of serial dependence in high-level face-specific processing. Overall, this highlights the role of serial dependence in facial identity and its functionality in stabilizing perception and recognition, its sensitivity to factors such as ethnicity, visual noise, and facial orientation, and its implications for neurodiverse populations.

The Turbett et al. studies are of particular relevance for this thesis because the previous face was always a no-response face, meaning that it was irrelevant to the current task, which challenges the emphasis on task relevance in serial dependence (Bae & Luck, 2020; Ceylan & Pascucci, 2023; Czoschke et al., 2019; Houborg et

al., 2023a, 2023b; Pascucci et al., 2019; Pascucci & Plomp, 2021). However, it was not the aim of Turbett et al. to investigate whether serial dependence in facial identity occurs independently of task relevance, so this was not explicitly addressed. In all three papers that are part of this thesis, I explicitly investigated whether serial dependence occurs when a previous face is categorized as irrelevant to the current task. Furthermore, the participants in Turbett et al. were familiarized with the faces prior to the experiments, whereas the faces in my studies were unfamiliar to the participants. As we will learn later, the way in which faces are judged and recognized differs for familiar and unfamiliar faces.

Neurophysiological evidence for serial dependence in facial identity

The neurophysiological evidence for serial dependence in facial identity is rather sparse. However, there is some evidence that specific frequency bands may play a role. In particular, alpha and beta power frequencies have been associated with serial dependence for faces (Bell et al., 2020; Murai et al., 2018). It is suggested that perceptual ambiguity related to serial dependence in faces depends on the phase of alpha oscillations (Murai et al., 2018), and that a perceptual prior related to face perception is communicated in beta oscillations (Bell et al., 2020). However, Bell et al. (2020) used a gender classification task, which may not adequately address the nuances involved in facial identity, and no behavioral serial dependence effects were obtained, which limits understanding of the results; the findings of Murai et al. (2018) are merely reported in a conference abstract. In Papers II and III, I examined face-related neural correlates to further substantiate the role of face processing in serial dependence facial identity effects. I further examined neural mechanisms related to working memory to determine their precise role in serial dependence in facial identity.

Theoretical explanations of serial dependence

Lately, visual perception has been conceptualized through two closely related frameworks: Bayesian inference and predictive coding. The Bayesian approach is concerned with the optimal integration of prior knowledge with sensory data (i.e., the likelihood) to arrive at the posterior, i.e. the final percept (Ma et al., 2023). Predictive coding, on the other hand, assumes that early sensory areas encode prediction errors and not the actual sensory input (Rao & Ballard, 1999). Although these theoretical frameworks are somewhat complementary in their focus and application, they are similar in that they assume that top-down predictions are used to interpret ambiguous sensory information and improve processing efficiency.

Bayesian observer

The mathematical theory of probability is a plausible method to successfully deal with reasoning about uncertainty. Viewing probabilities as degrees of belief or degrees of partial information is a plausible foundation from which to explore visual processing. In Bayesian models of perception, it is assumed that the brain uses a process of probabilistic inference to extract meaning from ambiguous and noisy sensory impressions (Geisler & Kersten, 2002; Ma et al., 2023). This means that current sensory impressions are combined with previous experiences to produce the best possible guess about the current state of the world. In practice, this works as follows: (1) the brain receives noisy and ambiguous sensory impressions, (2) previous experiences and knowledge about the state of the world are represented as priors, (3) the brain calculates the likelihood of several possible explanations for the sensory input based on the current state of the world and the available sensory evidence, (4) Bayes' theorem is used to update the brain's belief by integrating the prior and the likelihood, resulting in what is currently perceived, (5) the updated beliefs are used to inform the brain on how to act and respond to the environment. In some instances, Bayesian models incorporate an implicit decision rule determined by the expected gain specified in a utility function. Gain or utility is associated with each combination of the true state of the world and action. In the case of serial dependence, the decision rule may be: if the brain does not process each sensory input from the beginning, stability is gained, but at the cost of veridical perception. Bayesian models are useful in explaining how the brain resolves ambiguous and noisy sensory impressions and have been used to model serial dependence (Cicchini et al., 2018; Kalm & Norris, 2018; van Bergen & Jehee, 2019).

For example, Cicchini et al. (2018) showed that serial dependence in orientation can be well explained by a Bayesian observer model, in which the weighted sum of the previous and current stimulus reduces noise in the perception of the current stimulus, leading to greater accuracy and faster reaction times. In addition, Kalm and Norris (2018) showed that a Bayesian model in which not only the previous stimulus, but multiple states of stimulus history are incorporated in the current stimulus judgment. This is because observers cannot continuously infer a model of the sensory evidence and therefore treats the internal representation as the best guess of current perception.

Predictive coding

In predictive coding, the brain is thought to constantly make predictions about the sensory input it is likely to receive based on previous experience, context and internal models of the world. The predictions are sent from higher levels (cognitive, associative areas) to lower levels of the brain that process sensory information (Rao & Ballard, 1999). When the sensory input arrives, it is compared with the brain's predictions. The difference between the predicted input and the actual input is called

the prediction error. If the sensory input matches the prediction, the error is minimal. If it does not match, a larger prediction error is generated, signaling that something unexpected has occurred and that the brain's model of the world needs to be updated (Friston, 2005; Rao & Ballard, 1999; Spratling, 2017).

The brain uses top-down and bottom-up processing to continuously reduce prediction error. In top-down processing, the brain adjusts its predictions and internal models based on the errors it receives. Essentially, the brain updates its expectations to better match the incoming sensory information. In bottom-up processing, the sensory input itself is adjusted (e.g., through attention, sensory reinforcement) to minimize the prediction error. Similar to the Bayesian framework, some sensory impressions are considered more reliable than others. The brain therefore assigns more weight to sensory information that it considers reliable and certain. The brain dynamically adjusts the precision or reliability of different sensory signals and prioritizes them accordingly in the prediction process (Friston, 2005).

From the perspective of predictive coding, serial dependence may occur because the brain uses previous perceptual experiences as expectations for current stimuli. When a current stimulus is presented, it is compared against these predictions, and any discrepancy between the most recent and the current stimulus is processed as an error signal. If the brain anticipates a stimulus based on recent stimulus history, the perception of the current stimulus may be drawn toward this expectation. In this sense, serial dependence would reflect a phenomenon in which current perceptions tend to align closely with previous stimuli. Predictive processing supports a hierarchical view, in which sensory input at lower levels propagates to higher levels and vice versa, which may be consistent with serial dependence manifesting at multiple levels of processing.

Faces as a stimulus

In general, the perception and recognition of faces is a specific subset of object perception and recognition. The purpose of face perception and recognition is the processing and identification of individuals based on facial information, while object perception and recognition aim to process, identify and classify various objects (e.g., cars, animals, furniture) in general (Gazzaniga et al., 2019). Face perception and recognition are often used as examples of the brain's domain specificity, suggesting that specialized cognitive functions (and brain areas) have evolved to process very specific types of information, such as processing faces and only faces (Gazzaniga et al., 2019; McKone & Robbins, 2011). This chapter provides an overview of the perception and recognition of faces. The aim of this overview is to provide an understanding of the uniqueness of faces as stimuli and the specialized neural circuits that underlie the processing of faces.

Face perception and facial recognition

Faces convey various important information, and the processes and mechanisms used to interpret this information are complicated and specialized. Evolution has shaped faces to be uniquely variable, possibly to signal individual identity (Sheehan & Nachman, 2014). The variety of shapes and sizes of faces is remarkable, and they are endowed with a large number of muscles, adding to their complexity (Young & Bruce, 2023). Nevertheless, people can easily draw a variety of conclusions about personality traits, physical characteristics, emotional states and preferences of complete strangers based on facial features alone as well as quickly determine whether someone is a friend or a foe (Dobs et al., 2019; LeDoux, 1996; Longin et al., 2013; Phelps & LeDoux, 2005).

It is thought that the processing of faces occurs in a configurative manner (Maurer et al., 2002). This means that the different features of a face are not processed individually, but simultaneously. First-order relational configuration refers to the spatial arrangement of facial features, such as the positioning of the eyes above the nose and the nose above the mouth. Holistic configuration results from the integration of these facial components, while second-order relational configuration concerns the relative arrangement of these features within the first-order configuration (Maurer et al., 2002). Support for holistic processing of faces is

provided primarily by the part-whole effect (Tanaka & Farah, 1993) and the composite effect (Young et al., 1987). The part-whole effect shows that individuals recognize two facial components better when they are presented in the context of a complete face as compared to when they are viewed independently (Tanaka & Farah, 1993). The composite effect shows delays in facial recognition when one half of a chimeric face (i.e., a facial image artificially created by combining features or halves of two different faces) is aligned with an inconsistent counterpart as compared to when the two halves are not aligned. Similar to the part-whole effect, the composite effect illustrates that attempts to focus on individual facial components are affected by interference from other parts of the face, meaning that access to facial features may be limited and that processing occurs at a holistic level (Young et al., 1987).

Recognizing different faces requires detailed analysis to identify the subtle and unique differences between each face, even though all faces share a common basic T-shaped structure consisting of two eyes located above a nose and mouth. The ability to recognize faces is increasingly seen as a specialized visual skill that requires extensive training and practice to master. Similar to other forms of expertise, the ability to recognize faces likely arises through the interplay of hereditary factors and experiential learning (Emberson, 2017; Gauthier et al., 2014). Better facial recognition abilities are associated with superior skills in holistic processing during face learning and recognition. However, featural processing (i.e., processing the face by its distinct features) during recognition, but not during learning, also appears to contribute to these abilities, suggesting that these two strategies influence different stages of facial recognition (Leong et al., 2023).

Recognition of familiar faces is significantly more efficient and reliable than that of unfamiliar faces and is highly accurate even when facial images are severely degraded (Bruce et al., 2001). Conversely, recognition of unfamiliar faces is significantly impaired by external noise and variations in head position or lighting conditions, even when image quality is high (Bruce et al., 2001; Burton et al., 1999; Chen et al., 2015; Duchaine & Nakayama, 2006; Hancock et al., 2000). When recognizing unfamiliar faces, individuals tend to focus on external features of the face, such as head shape and hairstyle, rather than the actual face, whereas the recognition of familiar faces goes beyond purely facial information and activates associative networks of autobiographical information and emotional attachment (Gobbini et al., 2004; Young & Bruce, 2023). In all studies of the present thesis, unfamiliar faces were used as experimental stimuli for which the external features were excluded in order to ‘force’ processing of the shape and configuration of the internal features of the faces (Axelrod & Yovel, 2010).

As noted above, faces have many subtle and unique differences despite their similar structure. Norm-based coding provides an effective approach to represent visual patterns that have similar structural features but need to be distinguished by subtle variations that indicate different facial identities. The norm-based framework

captures the essence of each identity by encoding how it deviates from a prototype within a multidimensional face-space (Rhodes & Leopold, 2011). The stored representation can be likened to an angular measure, where both direction and magnitude are critical in determining the position of a face in this multidimensional space (Valentine, 1991; Valentine et al., 2016). Consequently, recognizing a face requires a comparison between the face in question and the dimensional profiles of previously encoded faces to determine whether a face with analogous physical features exists in face-space. When numerous faces with similar physical attributes are catalogued in face-space, greater precision is required for each individual physical attribute, resulting in a longer duration of the identification process and a higher probability of error (Young & Bruce, 2023).

The above highlights the intricate mechanisms underlying face perception, from holistic processing to the encoding of identities in a multidimensional face-space and illustrates the interplay between innate abilities and learned expertise in recognizing faces. The following will introduce the reader to the specialized neural circuitry underlying these intricate mechanisms.

The neural basis of face processing

There is broad agreement that the human brain has developed specialized neural circuits for processing faces, mainly located in the fusiform face area (FFA) in the temporal lobe. For instance, a now classic model developed by Haxby et al. (2000) describes specific neural regions associated with different aspects of face processing. This model suggests that face perception involves the simultaneous activation of several neural areas, which are divided into a 'core system' and an 'extended system'. The model comprises two distinct processing pathways. One pathway is associated with perceptual categorization and connects the inferior occipital cortex to the inferotemporal cortex, where stable facial features are represented. The other pathway is associated with social and emotional cues and connects the inferior occipital cortex to the superior temporal cortex, which is responsible for encoding the dynamic aspects of faces that result from the movement of facial features. Figure 5 illustrates the brain regions that according to Haxby et al. (2000) are thought to constitute the core of the face perception system. Within this model, the occipital face area (OFA), the FFA and the posterior superior temporal sulcus (STS) are known for their role in processing facial identity. The core system is thought to be involved in processing both familiar and unfamiliar faces, although it appears to respond slightly more strongly to familiar faces (Duchaine & Yovel, 2015; Gobbini & Haxby, 2007; Guntupalli et al., 2017; Natu & O'Toole, 2011; Pitcher et al., 2011).

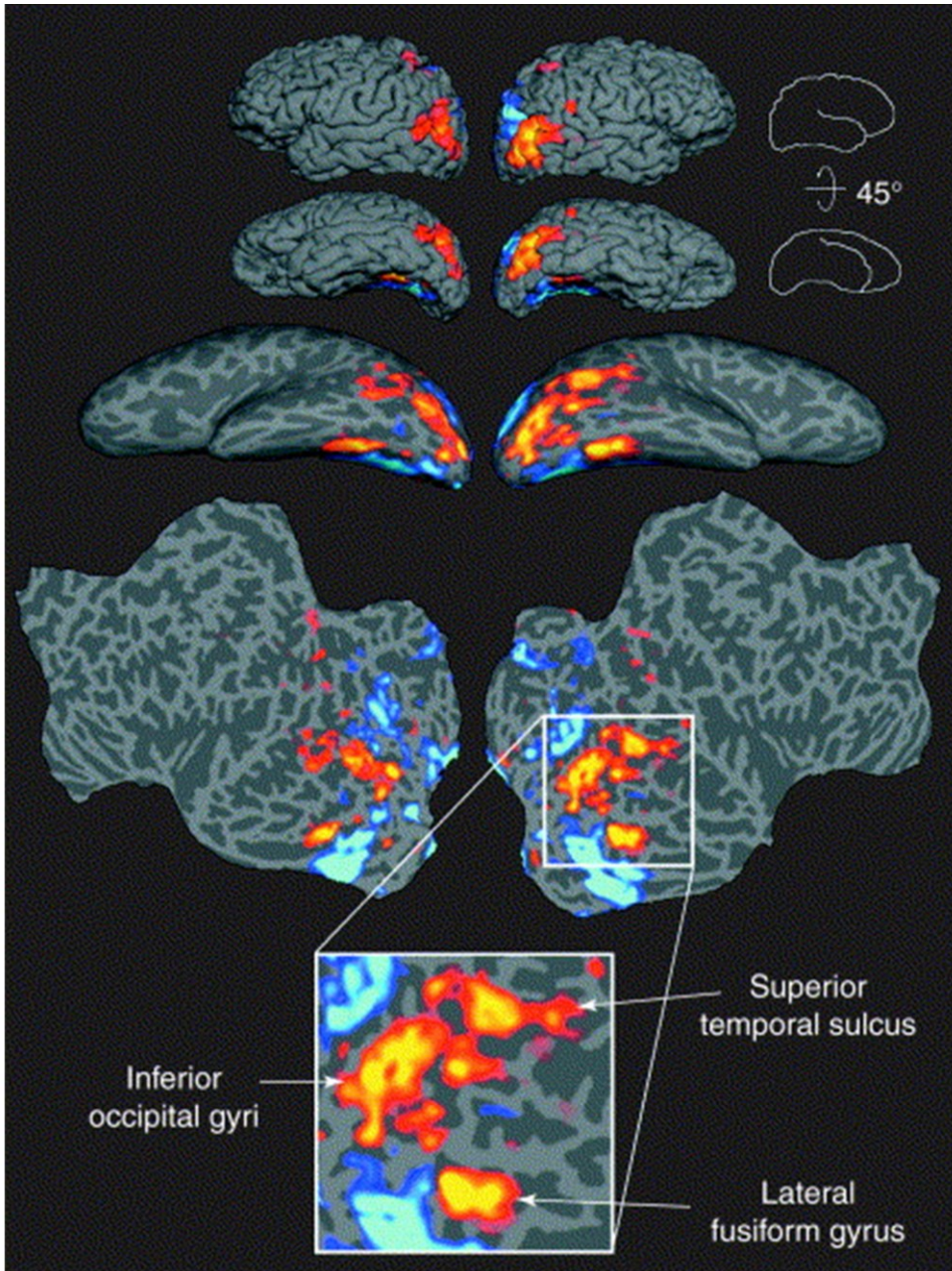


Figure 3 The core system of face perception

Areas in red to yellow reacted more to faces than houses. Areas in blue reacted more to houses than faces. The top figure shows lateral views of the folded cortical surface followed by the cortical surfaces of each hemisphere tilted back 45°. The cortical surfaces are then shown inflated with the cortex in the sulci in a darker shade of gray. Bottom figures show the cortical surface of each hemisphere, flattened into a two-dimensional sheet. Reprinted with permission from. The distributed neural system for face perception, Haxby et al. (2000). (Copyright © Elsevier, Published in Trends in Cognitive Sciences).

fMRI studies have shown that the lateral occipital gyri show selective activation in response to faces, highlighting the role of the OFA in analyzing facial shapes and features (Haxby et al., 2000; Fox et al., 2009; Rotshtein et al., 2005). The OFA is further thought to play an important role in the interpretation of second-order relational or configural cues that focus on the spatial relationships between facial features (Rhodes et al., 2009; Rotshtein et al., 2007). In addition, the fusiform gyrus is involved in processing these second-order relational cues related to faces (Rhodes et al., 2009; Rotshtein et al., 2007) but does not necessarily correspond to the region commonly referred to as the FFA (Maurer et al., 2007). When faces are turned upside down, responses of brain regions selective for faces, including the FFA, decreases slightly but significantly, and the activity of other areas selective for non-facial objects increases, supporting the view that the FFA is sensitive to the discrimination of individual faces (Rossion & Gauthier, 2002). Recently, the core system has been extended to include frontal regions of the brain such as the anterior fusiform gyrus, the anterior superior temporal sulcus and the inferior frontal gyrus, which to some extent challenges the view of the brain's domain specificity (Axelrod, 2016; Carlin et al., 2011; Collins & Olson, 2014; Duchaine & Yovel, 2015; Guntupalli et al., 2017; Pitcher et al., 2011; Rajimehr et al., 2009).

Nevertheless, Haxby et al.'s (2000) model provides a comprehensive framework that emphasizes both the specialization and integration of brain areas in face perception. It goes beyond the notion of a single 'face area' in the brain and describes a more nuanced system in which multiple regions contribute to different aspects of face processing. This model of face perception outlines a dual-stream system that includes both core and extended systems that work together to process the various features of a face and emphasizes the distributed and specialized nature of face processing in the brain.

Working memory, perception and attention

Visual processing rarely occurs in isolation but is a highly integrative process involving multiple areas of the brain that work together to interpret visual information. This chapter provides an overview of working memory and the interplay with perception and attention in stimulus processing as well as working memory and attention specifically with respect to faces.

Working memory

Working memory refers to a cognitive construct responsible for temporarily holding and manipulating information needed for complex tasks such as reasoning, learning, and problem-solving (Baddeley, 2003). Working memory plays a critical role in maintaining focus on specific tasks, even in the presence of distractions or competing stimuli (Cowan, 2006; Engle et al., 1999). Working memory is not about long-term storage, but rather about the temporary maintenance and manipulation of information that is currently needed for cognitive tasks. Working memory has limited capacity, meaning it can only hold and process a small amount of information at once. This limitation is often described in terms of ‘chunks’ of information (Thalman et al., 2019). A classic model proposed by cognitive psychologist George Miller (1956) suggests that the typical working memory capacity is about 7 ± 2 chunks of information, though this number can vary. The demands placed on working memory such as the complexity of the task or the amount of information maintained in working memory can influence its effectiveness (Ma et al., 2014). The following refers specifically to visual working memory.

The most acknowledged models of working memory capacity today are flexible resource models (Alvarez & Cavanagh, 2004; Ma et al., 2014) and discrete capacity models (Luck & Vogel, 1997; Vogel et al., 2001). Flexible resource models assume that a limited pool of working memory resources is continuously allocated. In these models, each memory representation has a certain amount of noise and allocating a greater amount of working memory resources results in less noise and

increases the resolution (quality) of the memory representation. Working memory capacity is limited because more information and more complex objects require a greater amount of resources as compared to less information and simpler objects, leaving fewer resources available to process additional information (Alvarez & Cavanagh, 2004; Ma et al., 2014). Discrete capacity models generally assume a fixed slot organization of working memory capacity, where each object is represented in one slot regardless of its complexity. When all slots are occupied, the limit of working memory capacity is reached (Luck & Vogel, 1997; Vogel et al., 2001). However, one item can also be assigned to multiple slots to reduce noise and improve the resolution of a memory representation by averaging over slots (Zhang & Luck, 2008). Irrespective of this, both models assume that the capacity of working memory is limited to three to four items (Luck & Vogel, 1997; Ma et al., 2014). One established way of measuring working memory capacity is by using Cowan's K , which reflects the number of items that can be maintained in working memory and also takes into account response bias due to guessing (Cowan, 2001). Cowan's K was used as a measure of working memory capacity in Paper II, which investigated the relation between serial dependence and working memory capacity.

Many models of working memory assume that once objects are encoded in working memory, they are independent of each other and do not interact (Alvarez & Cavanagh, 2004; Bays et al., 2009; Cowan, 2001; Fougner et al., 2012; Luck & Vogel, 1997). However, working memory is thought to maintain not only item-specific information but also group-level data, such as statistical summaries (Brady & Alvarez, 2011, 2015), and representations in working memory are thought to be susceptible to interference from concurrently maintained information (Huang & Sekuler, 2010; Oberauer & Lin, 2017; Rademaker et al., 2015). For example, Bae and Luck (2017) showed that similar orientations maintained in working memory tended to be repelled by each other, while dissimilar orientations were assimilated together. Moreover, when an orientation was given greater attentional priority by cues, its representation in memory was less influenced by other orientations. Conversely, orientations with lower attentional priority were strongly influenced by orientations with high priority. The above challenges the assumption of independence of objects in working memory and indicates relational encoding between objects maintained in working memory. Because working memory is thought to play a role in serial dependence, it was important to determine whether serial dependence can be separated from working memory interactions or is a by-product of such effects, which was investigated in Paper I.

The link between perception, working memory, and attention

Perception provides the sensory input necessary for working memory, and working memory maintains, updates, and transforms this information to guide behavior and decision-making (Awh et al., 2006). Perception helps determine what information enters working memory and narrows the focus on stimuli, allowing the brain to allocate resources for more efficient information processing (Gazzaley & Nobre, 2012). Historically, working memory was thought to influence perception through its shared neural substrate with selective attention, which is a function of the frontoparietal network (Awh et al., 2006; Chun et al., 2011; Courtney et al., 1997; Fuster, 2001; Lavie & de Fockert, 2005; Miller et al., 1996). However, recent evidence has shown that the link between perception and working memory goes beyond frontal brain regions and attentional selection mechanisms. It is thought that the content of working memory is maintained in the visual cortex (Emrich et al., 2013; Harrison & Tong, 2009; Rademaker et al., 2019). Furthermore, synaptic connections between neurons appear to preserve traces of working memory content from past events, which have been shown to influence perceptual processing of stimuli in subsequent tasks (Grill-Spector et al., 2006; Mongillo et al., 2008; Stokes, 2015). In addition, reentrant feedback from working memory has been shown to influence early stages of perceptual processing and modulate perceptual sensitivity between content maintained in working memory and stimuli in the visual field (Soto et al., 2010). For example, content maintained in working memory can influence external attention and stimulus detection during visual search (Downing & Dodds, 2004; Olivers et al., 2006; Kiyonaga & Egner, 2016; Sawaki & Luck, 2011) and directly alter the way a stimulus is perceived (Teng & Kravitz, 2019). Conversely, incoming visual information can interfere with working memory maintenance of previous stimuli and impair performance in, for example, change detection tasks and alter subsequent memory reports (Magnussen & Greenlee, 1992; Lorenc et al., 2018; Nemes et al., 2012; Rademaker et al., 2015; Wildegger et al., 2015). Working memory is also influenced by the quality of perceptual input, and without accurate perceptual input, working memory fails to function properly (Santana et al., 2013). Considering the reported presence of serial dependence effects in both perception and working memory and the known interactions between these two processes, Paper III sought to further understand the interactive contribution of perceptual and working memory processes to serial dependence in facial identity.

The visual environment contains a continuous stream of relevant and irrelevant sensory information. To enable goal-directed behavior, we must identify what is relevant and suppress what is irrelevant; perceptual attention plays a significant role in this process (Carrasco, 2011). There is a reciprocal relationship between working memory and attention, such that these two cognitive functions are interdependent. When attention is distracted or overloaded, the ability to maintain and process

information in working memory decreases. Conversely, external attention and perceptual processing suffer when working memory is depleted (Oberauer, 2019). Resource-based theories assume that attention is necessary for the limited capacity of working memory, while selective processing theories state that different forms of attention interact with working memory, focusing on attentional selection of working memory contents and the role of working memory in cognitive control (Oberauer, 2019). The concept of attention as a resource suggests that the cognitive system has a limited capacity that is divided and allocated according to the demands of a task, with the speed and accuracy of processing being directly proportional to the amount of resources allocated to the task (Navon & Gopher, 1979). The notion that working memory capacity reflects this limited resource has been widely supported, suggesting that working memory capacity fulfils functions typically associated with attention (Anderson et al., 1996; Case, 1972; Just & Carpenter, 1980; Ma et al., 2014; Oberauer, 2019). Various functions of this attentional resource such as storage and information processing, control of perceptual attention and memory maintenance have been highlighted (Allen et al., 2006; Ester et al., 2014; Just & Carpenter, 1992; Lavie, 2005).

Furthermore, working memory maintains task rules that regulate attentional selection mechanisms to recognize what information is relevant and irrelevant to a current goal (Engle & Kane, 2004; Kane et al., 2001; Kane & Engle, 2002; Oberauer, 2019; McCabe et al., 2010). When the capacity of working memory is depleted, perceptual attention suffers, which facilitates the influence of task-irrelevant information on current task goals (Carmel et al., 2012; de Fockert et al., 2001; Fukuda & Vogel, 2009; Fukuda et al., 2016; Gulbinaite et al., 2014; McNab & Klingberg, 2008; Robison et al., 2018; Vogel et al., 2005; Ye et al., 2018). There is a growing body of evidence to suggest that working memory load can influence the way in which individuals perceive and process incoming sensory information (Agam & Sekuler, 2007; Konstantinou et al., 2012; Konstantinou & Lavie, 2013, 2020; Michail et al., 2021; Soto et al., 2010; Tavares et al., 2016). When more items or more complex information is maintained in working memory, fewer resources are available for perceptual processing due to the shared pool of cognitive resources, which may lead to impaired perceptual performance (Carmel et al., 2012; de Fockert et al., 2001; Fukuda & Vogel, 2009; Fukuda et al., 2016; Gulbinaite et al., 2014; McNab & Klingberg, 2008; Robison et al., 2018; Vogel et al., 2005; Ye et al., 2018). When working memory load is high, the ability to process stimuli may be impaired, resulting in a reduced ability to perceive changes in the environment and stimulus discrimination may become less accurate (Carmel et al., 2012; de Fockert et al., 2001).

Individual differences in working memory capacity

Individual differences in working memory capacity are well documented. These differences are attributed to various factors, including differences in storage capacity and attentional selection mechanisms that control the maintenance, encoding and retrieval of task-relevant information (Unsworth, 2016). As compared to individuals with low working memory capacity, individuals with high working memory capacity tend to be better able to utilize attentional selection mechanisms to prevent task-irrelevant information from interfering with current task goals (Fukuda & Vogel, 2009; Fukuda et al., 2016; Gulbinaite et al., 2014; McNab & Klingberg, 2008; Robison et al., 2018; Vogel et al., 2005; Ye et al., 2018). For example, individuals with high working memory capacity can filter out information that is irrelevant to current task goals more effectively than individuals with low working memory capacity when relevant and irrelevant information is displayed simultaneously (Vogel et al., 2005; Ye et al., 2018).

In addition, individuals with high working memory capacity are less susceptible to proactive interference, i.e. the interference of previous memories on the current content of working memory, than individuals with low working memory capacity (Engle, 2002; Engle & Kane, 2004; Fournier et al., 2014; Kane et al., 2007; Redick, 2014). Studies on item-method directed forgetting (I-MDF), in which participants are cued to intentionally forget certain items after encoding, show that individuals with high working memory capacity have better control over information that is encoded and maintained in working memory as compared to those with low working memory capacity (Aslan et al., 2010; Marevic et al., 2018). Intentional forgetting is thought to involve the same attentional selection mechanisms used for external suppression of irrelevant information (Aron et al., 2003; Aron & Poldrack, 2006; Aron et al., 2004). This process requires greater effort and consequently greater working memory capacity than simply trying to remember information (Cheng et al., 2012; Fawcett et al., 2013; Wang et al., 2019).

The current evidence indicates that working memory plays a central role in cognitive processing and interacts closely with perception and attention regulation. Furthermore, individual differences in working memory capacity appear to have a significant impact on the interaction between working memory and perceptual attention. Given the characteristic feature of serial dependence, in which past sensory experiences that have lost their relevance influence subsequent perceptual judgments, it was reasonable to think that working memory capacity may play a central role in the occurrence of serial dependence effects. This was investigated in Paper II.

Working memory for faces

Due to their high complexity, working memory capacity for faces is thought to be more limited as compared to that of other visual objects with a maximum limit of one to two faces (Alvarez & Cavanagh, 2004; Curby & Gauthier, 2007; Eng et al., 2005). However, there are indications that working memory capacity for faces is influenced by facial similarity such that similar faces require more working memory capacity than different faces (Jiang et al., 2008). A greater number of upright as compared to inverted faces can be maintained in working memory (Curby & Gauthier, 2007), and memory precision for upright faces exceeds that for inverted faces (Lorenc et al., 2014; Krill et al., 2018). However, working memory for inverted faces appears to have an advantage over other non-facial objects (McKone & Robbins, 2011). In Paper II, I took advantage of the finding that working memory capacity is greater for inverted than for upright faces to determine whether the contribution of working memory processes to serial dependence is specific to working memory for faces.

The theoretical framework (Alvarez & Cavanagh, 2004; Luck et al., 1997; Ma et al., 2014; Vogel et al., 2001), which provides a distinction between working memory capacity in terms of slots and the resolution of representations, suggests that perceptual expertise may increase the resolution of representations in working memory (Scolari et al., 2008; Curby & Gauthier, 2010; Lorenc et al., 2014). Indeed, faces of one's own ethnicity are processed with greater precision and require less working memory capacity than faces of different ethnicities (Stelter & Degner, 2018; Young et al., 2012; Zhou et al., 2018). Furthermore, individuals with expert knowledge of different object categories and familiar faces have been shown to have greater working memory capacity than those with less expertise (Curby et al., 2009; Jackson & Raymond, 2008). These findings underline an important implication: resolution may be a particularly adaptive property of working memory for faces that can be influenced by perceptual experience. However, although working memory maintenance for faces has been shown to deteriorate significantly over time, the duration of the maintenance phase only appears to influence memory retrieval but not memory resolution (Krill et al., 2018).

Faces and attention

Human faces are among the most socially and biologically important stimuli we encounter, and there is evidence that in many circumstances faces attract and hold attention more effectively than many other types of visual stimuli (Carmel et al., 2012; Compton, 2003; de Fockert et al., 2001; Devue et al., 2012; Langton et al., 2008; Palermo & Rhodes, 2007; Sato & Kawahara, 2014). This phenomenon is

often referred to as face prioritization or face superiority in visual processing (Palermo & Rhodes, 2007). Faces have been shown to serve as powerful distractors that attract attention even when they are irrelevant to the task at hand (Carmel et al., 2012; de Fockert et al., 2001). For example, in studies where participants are asked to ignore faces and focus on other tasks, irrelevant faces often involuntarily attract attention and slow down reactions to the main task (Langton et al., 2008). Furthermore, studies using visual search experiments in which participants search for a target amidst distractors have shown that participants detect faces faster than other objects, even when the face is embedded in complex scenes (Cohen et al., 2017; Golan et al., 2014; Hershler & Hochstein, 2005; Langton et al., 2008; Mayer et al., 2015). Moreover, attending to a face may be sufficient for this face to be unintentionally maintained in working memory despite being irrelevant to the current task (Eitam et al., 2014; Schweinberger et al., 2004).

The indication is that faces are prioritized by attention for perceptual processing. So, due to the mediating role of attention in serial dependence effects, it was plausible to assume that a previously seen face that was merely perceived and explicitly categorized as irrelevant to the task at hand may still induce serial dependence on a subsequent face. This was initially investigated in Paper I and then further investigated in Papers II and III.

Method

Assessing serial dependence

Serial dependence is usually investigated by means of repeated measures psychophysical experiments in which consecutive stimuli are typically randomly drawn from a circular or linear morphed continuum (Manassi & Whitney, 2024). In this thesis, a circular morphed continuum between three facial identities was used and a facial matching task in which two consecutive facial images were randomly drawn from the morphed continuum formed the basis for the experimental procedures in all three papers. Serial dependence was assessed using a method of adjustment response, which is a classic psychophysical method first developed by Fechner (1860) to measure sensory thresholds. The method of adjustment response is a continuous matching response in which participants after each trial are instructed to adjust and reproduce one stimulus until it looks exactly like a previously seen target stimulus and then submit the adjusted stimulus as their response. During the experiments, participants adjust the stimulus autonomously and are generally allowed to make repeated adjustments based on their subjective judgments, with no limit on the direction or number of adjustments. The physical appearance of the stimulus changes continuously based on a predetermined minimum change. The two consecutive facial images in all three papers were always presented within the same trial and the second face was always the target face that was reproduced in the adjustment response. The first face was therefore a no-response face that participants were instructed to attend to but not memorize, except in Experiment 2, Paper I, in which I investigated whether serial dependence may be separated from interactions within working memory.

Statistical analyses of serial dependence

Serial dependence analyses depend on the psychophysical task (Pascucci et al., 2023). However, irrespective of the task, the analyses involve quantifying the systematic relationship between the response to a current target stimulus and one or several stimuli presented prior to the target stimulus. Because an adjustment response was used in the present work, the following applies to these tasks. Prior to analyses, adjustment errors, which refer to the difference in morph steps (one morph step corresponds to one morphed image between two images in the morphed continuum) between the response and the target stimulus, are calculated and

corrected for outliers, which could be due to, for example, attention deficits by excluding trials in which the adjustment errors lie outside a predefined threshold. Reaction times in the adjustment task that exceed or fall below a predefined threshold are also excluded from the analysis (e.g., Liberman et al., 2014). For the statistical analysis, parameter estimation procedures are frequently used in which a simplified first Derivative of Gaussian (DoG) function is fitted to the data (e.g., Fischer & Whitney, 2014; Liberman et al., 2014). The DoG function is an important concept in many fields such as image processing, signal processing, and computer vision and fitting this function to data results in an antisymmetric curve that emphasizes areas of rapid intensity change (Romeny, 2003).

Serial dependence magnitude is estimated by fitting the DoG to the adjustment errors as a function of the difference in morph steps between the target stimulus and a preceding stimulus, resulting in an amplitude measure that reflects the magnitude of serial dependence. The amplitude measure is usually expressed as the half-amplitude, i.e., the highest point of the resulting curve between peak and zero. Figure 4 shows a graphical illustration of the DoG fitted to serial dependence data in Experiment 1, Paper I.

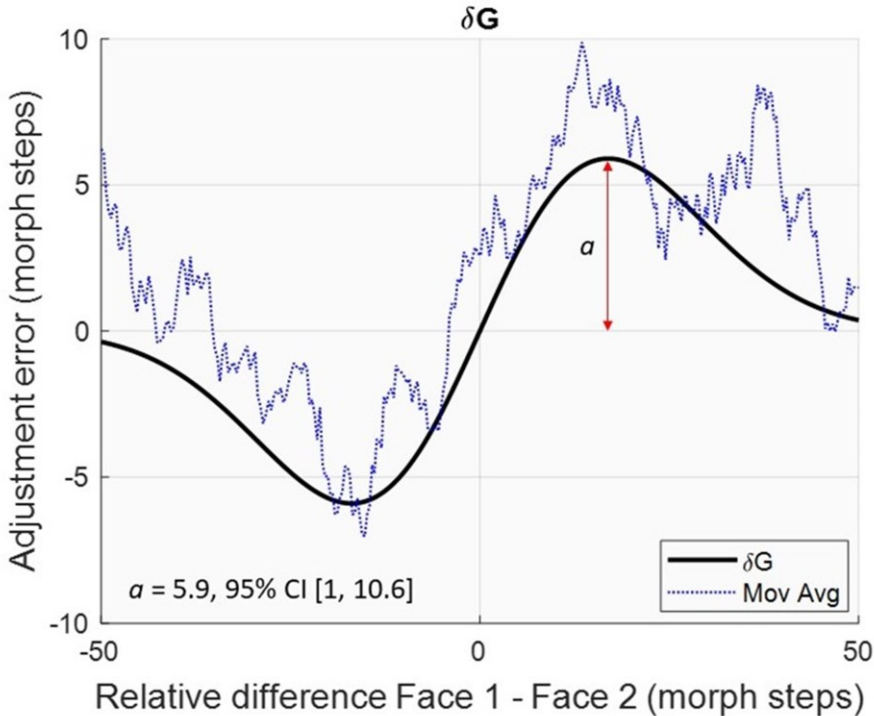


Figure 4 Derivative of Gaussian (δG)

The signed adjustment errors are displayed on the ordinate and the signed difference between a target face (Face 2) and a previous face (Face 1) is shown on the abscissa. The half-amplitude of serial dependence is represented by a . The dashed blue line represents the moving average. The model fit represented by the black line shows how serial dependence increases from a relative difference of zero morph steps to approximately twenty-five morph step differences between the current and previous face and then starts to fade. Reprinted from Serial dependence in facial identity perception and visual working memory, Lidström, 2023 (Copyright © The author, published in Attention, Perception and Psychophysics. This article is distributed under a Creative Commons CC BY license).

In Paper I and II, a DoG function following the procedures described by Johansson (2020) was used to analyze the data. This DoG function was defined as:

$$y = f(x)\mu\sigma\alpha$$

where $f(x)$ represents a normal probability density function with mean μ and standard deviation σ . y represents each trial's adjustment error and x represent the difference between a target stimulus and a previously presented stimulus. α is a parameter that, when multiplied by $f(x)x$, the first derivative of the Gaussian function, affects the height of the curve. The σ parameter controls the width of the curve.

Because serial dependence is often accompanied by repulsive effects when previous stimuli differ almost maximally from current stimuli, which the DoG cannot account

for (Bliss et al., 2017), the DoG is often supplemented by a nonparametric procedure. The nonparametric procedure can be based on categorical classification errors, in which the morphed continuum is divided into categories and the percentage of classification errors when the response to a target stimulus falls within the category boundaries of the previous stimulus is estimated and subsequently used as a measure of serial dependence (Manassi et al., 2019). This nonparametric approach was used as a supplement to the DoG in Papers I and II. The reader is referred to Paper I for a detailed description of this procedure as applied to serial dependence facial identity effects. A different nonparametric approach to analyzing serial dependence data has also been developed, in which the median or mean signed adjustment errors are calculated within a range of signed stimulus difference values and positive adjustment errors are subtracted from negative adjustment errors (Samaha et al., 2019). This results in a measure for each participant that shows the systematic deviation in adjustment errors from zero in which, similar to the categorical analysis, positive values are regarded as serial dependence and negative values as repulsive effects. This approach is suitable for small sample sizes and was used in Paper III to determine a reliable measure of serial dependence for each participant. A more detailed description of this procedure is outlined in Paper III.

Electroencephalogram

In Papers II and III, EEG was used to investigate the underlying neural mechanisms contributing to serial dependence. EEG is an electrophysiological technique for recording the electrical activity of the brain (Berger, 1929). EEG is a powerful method for the non-invasive investigation of the electrophysiological dynamics of the brain and for linking those dynamics to cognition. EEG measures the electrical activity of large parts of the brain by macroscopic electrodes placed on the surface of the scalp and is advantageous because of its high temporal resolution and the direct measurement of neural activity at the population level in humans (Cohen, 2017). EEG measures postsynaptic potentials, which are generated by slow currents after the release of neurotransmitters at the terminal end of an axon. The fluctuations in oscillatory activity measured by EEG depend on the synchronized or desynchronized activity of underlying neural populations (Biasucci et al., 2019). ERPs and TFRs (described below) are commonly studied neurophysiological measurements that can be derived from EEG data. Both ERP and TFR analyses were conducted in Papers II and III. Statistical analyses between experimental conditions for ERP and TFR data were conducted using a nonparametric cluster-based procedure (Maris & Oostenveld, 2007), which is outlined in Papers II and III.

Event-related potentials

ERPs are very small voltages generated in the brain structures in response to specific events or stimuli (Blackwood & Muir, 1990). ERPs are EEG changes that are time locked to sensory, motor or cognitive events, and are thought to reflect the summed activity of postsynaptic potentials that occur when large numbers of similarly oriented cortical pyramidal neurons fire synchronously when processing information (Peterson et al., 1995). ERP waveforms are described in terms of latency and amplitude and can be divided into two categories. Early sensory components, which peak within approximately the first 100 ms after the stimulus and are largely dependent on the physical parameters of the stimulus. ERPs generated in later stages reflect information processing and stimulus evaluation (Luck, 2014). In Paper II, all ERPs of interest were preselected, while only some of the ERPs of interest were preselected in Paper III, as the analytical approach for the EEG data was exploratory. The ERPs that were preselected in Papers II and III are described in the following, while the ERPs identified in the exploratory analyses in Paper III are interpreted and described in the General discussion.

Preselected ERPs associated with face processing

ERPs can reflect different stages of neural processing related to the perception and recognition of faces (Olivares et al., 2015). The most well-known ERP component associated with the processing of faces is the N170. The N170 is a negative deflection in the ERP waveform that occurs ~ 170 ms after the presentation of a face and is particularly large and pronounced over the occipitotemporal scalp areas, especially the right hemisphere (right fusiform gyrus). The N170 component is thought to reflect early structural encoding of faces (e.g., eyes, mouth and overall facial configuration, Bentin & Deouell, 2000). The amplitude of the N170 component is modulated by working memory load during the processing of faces and has been associated with individual differences in working memory capacity (MacNamara et al., 2012; Morgan et al., 2008). Furthermore, this component is thought to be sensitive to attention to faces and facial visibility and the ability to extract and accumulate information necessary for recognition (Eimer, 2000; Holmes et al., 2003; Jemel et al., 2003; Philiastides et al., 2006; Rousset et al., 2008; Sreenivasan et al., 2009). The N170 was relevant in Paper II, in which the consecutive faces were viewed under simultaneous working memory load, and in Paper III, in which I manipulated the visibility of the faces.

The subsequent P200, which shows a positive deflection over occipitotemporal regions ~ 200 ms after stimulus onset, is also associated with face processing. It has been suggested that this component is sensitive to the typicality of faces and reflects the encoding of second-order spatial relations and is associated with norm-based encoding of faces (Schweinberger & Neumann, 2016; Wuttke & Schweinberger, 2019). The P200 is also sensitive to the visibility of faces and is amplified when

visibility is reduced, presumably reflecting increased perceptual processing demands (Bankó et al., 2011). The effect of perceptual demands on serial dependence in facial identity was relevant in Paper III, where I focused on the P200 component.

Preselected ERPs associated with working memory

Several ERP components are associated with working memory processes that reflect how the brain supports encoding, maintenance, and retrieval of information (Drew et al., 2006). In Paper II, which investigated relations between working memory processes and serial dependence, the focus was specifically on one of these components, called the negative slow wave (NSW), which is thought to reflect working memory maintenance.

The NSW is a sustained slow ERP component observed in tasks involving the maintenance and manipulation of working memory contents and manifests between ~ 200 and 1,000 ms post stimulus onset (Bosch et al., 2001; Mecklinger & Müller, 1996; Ruchkin et al., 1990, 1995). The NSW is often recorded at frontal scalp sites, but there is a notable difference in the scalp distribution of the NSW between spatial and object memory tasks, suggesting that these two types of working memory rely on somewhat different neural substrates (Mecklinger & Pfeifer, 1996). Specifically, the NSW for spatial working memory is mainly localized over the posterior parietal and occipital lobes, whereas the NSW for object working memory is characterized by a topography in the mid-frontal area of the scalp. The amplitude of the NSW has been shown to increase with increasing working memory load and asymptotes when working memory capacity is reached, suggesting that it is sensitive to the number of items maintained in working memory (Fukuda et al., 2015; Perez & Vogel, 2012). The NSW is also closely associated with individual differences in working memory capacity (Fukuda et al., 2015).

Time-frequency representations

Oscillatory activity is widely thought to act as the brain's 'timing system' for communication and function. Oscillations enable the coordination and synchronization of activity between different regions of the brain so that neurons can process information efficiently. Their rhythms can be transient (short-lived) or sustained over time (Cohen, 2017). EEG data in the time domain can be transformed into TFRs that reflect dynamic changes within specific frequency bands in response to events of interest (Cohen, 2014). TFR approaches, also referred to as spectral analyses, can reveal neurocognitive phenomena that are overlooked by EEG analysis techniques such as ERPs. Spectral analysis techniques are useful for assessing both the presence of oscillatory patterns within a single time series and the synchronization of oscillations across two different time series. Spectral analysis

reveals two important features inherent to the time series. The first feature is that EEG data show a higher concentration of energy at lower frequencies as compared to higher frequencies, which is due to autocorrelations in the time series; in particular, the voltage at a given time point depends on the voltage recorded at the previous time point (Kahana, 2006). Oscillatory power is categorized according to frequency bands, measured in Hertz (Hz). Frequency bands associated with working memory processing were of particular relevance to Papers II and III, in which I investigated the effects of working memory load on oscillatory power to explore the neural processes that contributed to serial dependence.

Frequency bands associated with working memory

The frequency bands most commonly associated with working memory are frontal theta (4 to 7 Hz) and posterior alpha (8 to 13 Hz) and beta (13 to 30 Hz) power (Erickson et al., 2019; Fukuda et al., 2016; Hsieh & Ranganath, 2014; Pavlov & Kotchoubey, 2022; van Ede et al., 2017). Because lower beta power “can be considered the ‘fast’ brother of alpha” (Michelmann et al., 2022), these will be referred to as alpha / beta in the following. Frontal theta power is typically amplified with increased working memory load (Jensen & Tesche, 2002) and is also thought to be “a lingua franca for cognitive control” (Eisma et al., 2021). The processing of complex and information-rich content generally leads to attenuation of alpha / beta power (Michelmann et al., 2022). Posterior alpha / beta power is thought to track the number of objects maintained in working memory and are typically attenuated as the number of objects maintained in working memory increases (Busch & Herrmann, 2003; Fukuda et al., 2015; Sauseng et al., 2009; van Ede, 2018). However, frontal alpha / beta power is also amplified during the maintenance of task-relevant information in working memory and may also reflect decoupling of sensory areas to protect internal memory representations from interference (Manza et al., 2014; Riley & Constantinidis, 2016; van Ede, 2018).

Summary of research studies

The overarching aim of this thesis is to advance understanding of how perceptual and working memory processes contribute to serial dependence in facial identity. Paper I focused on the temporal dynamics of serial dependence in the context of task-related decisions and whether and how such effects can be separated from serial effects arising from working memory interactions. Paper II focused on the relationship between serial dependence and working memory capacity and investigated the neural mechanisms underlying this relationship. Finally, Paper III aimed to better understand the interactive contribution of perceptual and working memory processes to serial dependence in facial identity and the neural mechanisms underlying these processes.

Paper I

Background Experiment 1

The aim of Experiment 1 was to investigate the temporal dynamics of serial dependence facial identity effects in the context of task-related decisions. Previous findings based on non-facial stimuli emphasize the importance of task relevance and higher-order cognitive functions, such as working memory and decision processes in serial dependence effects (Bae & Luck, 2020; Bliss et al., 2017; Czoschke et al., 2019; Fritsche et al., 2017; Pascucci et al., 2019; Pascucci & Plomp, 2021). Faces are behaviorally relevant and there are several indications that faces have priority access to attention (Compton, 2003; Devue et al., 2012; Palermo & Rhodes, 2007; Sato & Kawahara, 2014) and can be unintentionally maintained in working memory even though they are irrelevant to the task at hand (Eitam et al., 2014; Schweinberger et al., 2004). Therefore, I expected that a previous face that was merely perceived and explicitly categorized as irrelevant to the adjustment task would still induce serial dependence. The temporal dynamics of serial dependence were examined to shed new light on the time course of serial dependence in facial identity.

Methods and procedure Experiment 1

In Experiment 1, participants were shown two consecutive facial images separated by an interstimulus interval (ISI) of 1, 3, 6, or 10 s, and were instructed to reproduce

the second face using an adjustment response after a varying response delay of 0, 1, 3, 6, or 10 s (Bliss et al., 2017). Participants were explicitly informed that the first face was irrelevant to the adjustment task and should be attended to but not memorized, and that the second face was the target face to be memorized and responded to. Data were divided into conditions by ISI \times response delay and analyzed using a DoG and nonparametric categorical analysis. DoG analyses were also used to assess serial dependence effects resulting from the stimuli and the response of the previous trial for each condition.

Results and discussion Experiment 1

Serial dependence occurred even though participants were explicitly informed that the first face was irrelevant to the adjustment task, suggesting that the first face was unintentionally maintained in working memory (Eitam et al., 2014; Schweinberger et al., 2004). No serial dependence from the stimuli or response of the previous trial was obtained, contradicting the importance of task relevance in serial dependence (Bae & Luck, 2020; Bliss et al., 2017; Czoschke et al., 2019; Fritsche et al., 2017; Pascucci et al., 2019; Pascucci & Plomp, 2021). Serial dependence was only obtained at a short ISI of 1 s: no significant effect was observed at ISIs of 3 s or longer, supporting that facial identity is expected to remain stable within brief temporal delays (Burr & Cicchini, 2014). An interaction between ISI and response delay showed that serial dependence occurred at response delays of 1 and 6 s, whereas no significant effect was obtained at response delays of 0, 3 and 10 s. This indicates that both perceptual and working memory processes (Bliss et al., 2017; Cicchini et al., 2017; Fritsche et al., 2017; Manassi et al., 2018), operating in different time windows, contributed to the effects. The results further suggest that within a 3 s time window, working memory representations are fragile and overwritten by subsequently processed stimuli (Sligte et al., 2008, 2010), which prevents serial dependence from taking full effect.

Background Experiment 2

Because serial effects can also emerge from interactions within working memory (Bae & Luck, 2017), the aim of Experiment 2 was to investigate whether serial dependence effects differ from interactions within working memory. If interactions within working memory occurred, I expected the second face to influence adjustment responses to the first face when both faces were task-relevant, as this face was already perceived and maintained in working memory when the second face was presented (Bae & Luck, 2017).

Methods and procedure Experiment 2

The experimental procedure was the same as in Experiment 1, except for the following changes: The ISI was held constant at 1 s, and to separate serial dependence from working memory interactions, participants were post-cued to

reproduce either the first or the second face. So, the adjustment response was made to the first face on 50 % of the trials. The response delays in this experiment were set to 1, 3 and 6 s to investigate whether the temporal dynamics obtained in Experiment 1 would be repeated. Both faces had to be maintained during the response delay, as the cue to which face to respond to was presented at the end of the response delay. The statistical analyses were the same as in Experiment 1, except that data were divided into conditions by target face (first / second) \times response delay.

Results and discussion Experiment 2

The results of Experiment 2 confirmed the temporal dynamics of serial dependence observed in Experiment 1 when responses were made to the second face. Serial dependence occurred most consistently for response delays of 1 and 6 s, whereas no significant effect was obtained for the 3 s response delay, suggesting that the temporal dynamics are the same regardless of whether a previous face is unintentionally or actively maintained in working memory. When responding to the first face, nonparametric analysis showed a significant serial effect at response delays of 1 and 3 s with a linear decrease from 1 to 6 s, suggesting that interactions within working memory occurred. These results were not confirmed by the DoG analysis, possibly indicating that this function is more suitable for analyzing serial dependence rather than working memory interactions. No serial dependence effects emerging from the stimuli or response of the previous trial were detected in any of the experimental conditions.

Overall, the main contribution of Paper I is that serial dependence in facial identity occurs independently of task-related decision processes with distinct temporal dynamics and may rely on mechanisms that are separate from those of working memory interactions.

Paper II

Background

Paper II investigated the contribution of working memory processing to serial dependence in facial identity. Working memory is closely linked to attentional control mechanisms, and individual differences in working memory capacity may influence this interaction, particularly how irrelevant information affects current task goals when working memory capacity is depleted (Carmel et al., 2012; de Fockert et al., 2001; Fukuda & Vogel, 2009; Fukuda et al., 2016; Gulbinaite et al., 2014; McNab & Klingberg, 2008; Robison et al., 2018; Vogel et al., 2005; Ye et al., 2018). Considering the characteristic feature of serial dependence, in which past sensory input that has lost its relevance has an influence on current perceptual judgments, working memory capacity may play a role in serial dependence effects.

To investigate this, I conducted a dual-task experiment comprising a task with varying working memory load that overlapped with the facial matching task used to assess serial dependence. I took advantage of the high temporal resolution of EEG, which enabled ERP and TFR analyses to assess the contribution of mechanisms related to perceptual attention and working memory to the manifestation of serial dependence in facial identity. To this end, I examined the face-related N170 ERP component as an index of perceptual attention (Eimer, 2000; Holmes et al., 2003) and focused on the NSW as an index of working memory maintenance (Mecklinger & Pfeifer, 1996). In addition, I explored induced theta and alpha / beta power, as working memory processes have previously been associated with this power spectrum (Cavanagh & Frank, 2014; Chen et al., 2022; Fukuda et al., 2015).

If working memory and attentional selection rely on shared resources (Oberauer, 2019), I expected selective suppression of the first face, that was irrelevant to the adjustment task, to be impaired, leading to greater serial dependence as working memory load increased. In this regard, I expected a reduced N170 response and an amplified NSW response for the first face with increased working memory load and stronger serial dependence. Furthermore, I expected participants with high working memory capacity to be less susceptible to serial dependence, as they are better able to prevent the influence of task irrelevant stimuli on current task goals than participants with low working memory capacity (e.g., Vogel et al., 2005; Ye et al., 2018).

Methods and procedure

A working memory task with three levels of working memory overlapped with the facial matching task in which two consecutive faces were presented, the second of which was reproduced in the adjustment task. Participants were explicitly informed that the first face was irrelevant to the adjustment task. Prior to the presentation of the consecutive faces, participants memorized 1, 2 or 3 cartoon face(s) (low / medium / high working memory load), which they maintained in working memory until the end of the trial when their memory for the cartoon face(s) was tested in a recall task. The cartoon face(s) were presented in inverted position on 50 % of the trials to determine whether the effect of working memory load on serial dependence reflects a general interaction or is specific to working memory for faces. EEG was recorded throughout the experimental session. Because no significant differences in performance in the working memory task or serial dependence were obtained between the upright and inverted cartoon faces, data were averaged across these conditions resulting in three conditions of low / medium / high working memory load. Serial dependence analyses within each condition were conducted using a DoG and nonparametric categorical analysis. Differences in serial dependence between conditions were analyzed by means of repeated measures analysis of variance (ANOVA). To investigate relations between working memory capacity and serial dependence, individual measures of serial dependence and adjustment

errors were regressed on individual measures of working memory capacity (Cowan's K). Behavioral measures of serial dependence were also regressed on the EEG effects obtained from ERP and TFR analyses to determine whether the neural mechanisms underlying these effects contributed to serial dependence.

Results and discussion

The behavioral results showed that the magnitude of serial dependence increased with increasing working memory load and that working memory capacity predicted serial dependence, suggesting that serial dependence is more likely to manifest when working memory capacity is depleted. In addition, working memory capacity significantly predicted adjustment errors, suggesting that participants with high as compared to low working memory capacity were better at maintaining or retrieving the task-relevant face. On average, amplified fronto-central negativity manifested as a NSW with respect to the first face at high working memory load and was directly related to serial dependence. The NSW was observed exclusively for participants with high working memory capacity, which is consistent with serial dependence only occurring at high working memory load for those participants. No significant difference in NSW amplitude was observed between low and high working memory load for participants with low working memory capacity, for whom serial dependence occurred regardless of working memory load. These results are consistent with the notion that mere attention to a face may facilitate automatic encoding of facial identities in working memory when working memory load is high (Carmel et al., 2012; de Fockert et al., 2001), and that participants with high working memory capacity are better able to prevent task irrelevant stimuli from interfering with goal-directed performance than participants with low working memory capacity (Aslan et al., 2010; Fukuda & Vogel, 2009; Fukuda et al., 2016; Gulbinaite et al., 2014; Marevic et al., 2018; McNab & Klingberg, 2008; Robison et al., 2018; Vogel et al., 2005; Ye et al., 2018).

The N170 amplitude elicited by both faces decreased with increasing working memory load, but the effect of working memory load on the N170 was similar for both faces. However, individual differences in N170 amplitude due to variations in working memory load for the first face predicted serial dependence independent of working memory capacity. Participants who showed similar N170 effects between low and high working memory load exhibited weaker serial dependence, while those who showed greater differences exhibited stronger serial dependence. This result may be due to successful attentional suppression of the first face regardless of working memory load or to individual differences in perceptual capacity (Eays & Lavie, 2018; Ward, 2019), as working memory load may have impaired perceptual processing (Grill-Spector et al., 2006; Guo et al., 2021; Landman et al., 2003; Mongillo et al., 2008; Sligte et al., 2008; Stokes, 2015; Vandembroucke et al., 2014). Although significant differences in theta and alpha / beta power due to

variations in working memory load were associated with working memory capacity, these effects were not related to serial dependence.

Overall, Paper II shows that working memory capacity contributes to serial dependence in facial identity in terms of selective suppression of task-irrelevant and selective maintenance of task-relevant information and suggests that the relation between working memory capacity and serial dependence is mediated by task demands. Furthermore, perceptual processing of a previously seen task-irrelevant face, independent of working memory capacity, appear to have contributed to the observed serial dependence effects.

Paper III

Background

Paper III (submitted) investigated the interactive contribution of perception and working memory to serial dependence in facial identity. Serial dependence is thought to occur at multiple levels of processing in the brain, from low-level sensory processing to high-level cognitive mechanisms, such as working memory (Manassi & Whitney, 2024). Perception and working memory are closely linked, as evidenced by a reciprocal relationship between the information maintained in working memory and various perceptual tasks (Gayet et al., 2013; Olivers et al., 2006; Soto et al., 2005; Teng & Kravitz, 2019; Teng & Postle, 2021) and a shared neural substrate in the visual cortex (Emrich et al., 2013; Harrison & Tong, 2009; Rademaker et al., 2019). Perceptual serial dependence is known to increase with increased sensory processing (Manassi et al., 2018), and as shown in Paper II, serial dependence also increased with increased working memory load. In Paper III, I used a dual-task experiment in which both perceptual and working memory demands were manipulated and EEG was used to explore the interactive contribution of perceptual and working memory processes to serial dependence in facial identity. I expected that facial identities processed under high perceptual and working memory demands would lead to stronger serial dependence than those processed under low perceptual and working memory demands. I had no predictions as to whether perception or working memory would contribute more to serial dependence or whether the effect would be due to an interaction between the two.

Methods and procedure

To assess serial dependence, I used a facial matching task in which two consecutive faces were presented, the second of which was reproduced in the adjustment task. To manipulate perceptual demands, the faces were superimposed with a scene image of 75 % (low demand) or 50 % (high demand) transparency (Sreenivasan et al., 2009). During the maintenance phase of the second face and overlapping with the

adjustment task, a memory task with two levels of working memory load was interspersed to manipulate working memory demands. 1 (low demand) and 3 (high demand) cartoon faces were used as load stimuli in the working memory task. Serial dependence was analyzed according to four conditions: low working memory demand, high working memory demand, low perceptual demand, high perceptual demand, using a nonparametric approach. Differences in serial dependence, adjustment errors and performance in the working memory task between experimental conditions were analyzed using two-way repeated measures ANOVAs with processing level (perception / working memory) and demand (low / high) as within participant factors. Correlation analysis between serial dependence manifesting due to perceptual and working memory demands was performed to assess their covariation. For the analysis of the EEG data, an exploratory approach was used in which the obtained behavioral serial dependence effects due to variations in perceptual and working memory demands were separately regressed on ERP and time-frequency data from the onset of the first face up until the adjustment response. In this way, time windows and channels that predicted serial dependence were identified in the EEG data which allowed me to identify the neural mechanisms underlying serial dependence. To determine the contribution of face-specific perceptual processing to serial dependence, I also investigated the effects of perceptual demands on the N170 and P200 ERPs, as they are known to be altered by facial visibility and are associated with behavioral deficits in face perception (Bankó et al., 2011; Jemel et al., 2003, Rousselet et al., 2008; Sreenivasan et al., 2009). Finally, regression analyses were conducted to determine relations between the mechanisms underlying the obtained EEG effects in terms of their contribution to serial dependence.

Results and discussion

The behavioral results showed that serial dependence increased with increased perceptual and working memory demands, but no interaction or covariation was obtained between the two, suggesting that serial dependence effects due to variations in perceptual and WM demands are independent. Performance in the working memory task decreased with increased working memory, but not perceptual demand, whereas no differences in adjustment errors in the facial matching task due to variations in perceptual and working memory demands were obtained.

The mechanisms associated with the EEG effects identified in the exploratory analysis are discussed in more detail in the General discussion. With respect to the first face, two ERP effects were identified that were positively associated with serial dependence. The first ERP showed amplified fronto-central negativity at high as compared to low perceptual demand for which serial dependence was more pronounced ~ 400 to 500 ms after stimulus onset, possibly reflecting impaired inhibition of the first face due to competing attention between stimulus processing

and inhibitory mechanisms at high perceptual demand (Alfonso & Menor, 2021; Kissler & Hauswald, 2022; Hauswald et al., 2011; Zanto & Gazzaley, 2009). Alternatively, this ERP may reflect the FN400 ERP and a familiarity effect due to the manipulation of facial visibility, such that a less visible face was considered less familiar and required more processing effort, also leading to competition between stimulus processing and inhibitory mechanisms (Bader et al., 2010; Bridger et al., 2012; Carrasco, 2011; Manahova et al., 2018). The second ERP showed greater central-parietal negativity at high as compared to low perceptual demand ~ 700 to 800 ms after stimulus onset, possibly reflecting a NSW and unintentional maintenance of the first face in working memory (Mecklinger & Pfeifer, 1996). The ERP results for the first face indicate that inhibitory mechanisms were impaired at high perceptual demand, leading to unintentional maintenance of the first face in working memory, subsequently affecting processing of the second face, contributing to serial dependence.

With respect to the second face, three ERP effects were identified that were positively associated with serial dependence. The first ERP showed greater positivity over the right parietal region at high as compared to low perceptual demand, where serial dependence was more pronounced ~ 300 to 350 ms after stimulus onset. This likely reflects the N250r ERP and depleted perceptual processing capacity due to parallel processing of the scene image and face at high perceptual demand (Eayrs & Lavie, 2018; Lavie et al, 2003; Neumann & Schweinberger, 2009), leading to stimulus uncertainty for the second face and greater dependence on the first face. The second ERP showed greater negativity over the left parieto-occipital region at high as compared to low perceptual demand ~ 585 to 635 ms after stimulus onset, which may reflect impaired selective rehearsal or impaired recollection for the second face (Alfonso & Menor, 2021; Kissler & Hauswald, 2022), resulting in internal stimulus uncertainty that contributed to serial dependence. The third ERP showed greater negativity over the right fronto-central region at high as compared to low perceptual demand ~ 1,100 to 1,140 ms after stimulus onset, possibly reflecting impaired post-retrieval monitoring (Hayama et al., 2008; Wilding, 1999; Wilding & Rugg, 1996), further increasing internal uncertainty, leading to serial dependence. The second ERP predicted the third ERP, which may indicate that impairment in selective rehearsal or recall led to impairment in post-retrieval monitoring for the second face, increasing uncertainty about successful retrieval, causing greater reliance on the first face, contributing to serial dependence. The N170 effect for the second face was marginally positively associated with serial dependence and with the second ERP for this face. This could indicate that deficits in perceptual processing caused impaired recollection or selective rehearsal, which jointly contributed to serial dependence, also due to stimulus uncertainty. The P200 effects for the faces were not associated with serial dependence.

Finally, attenuation of frontal alpha power during the maintenance phase of the second face was associated with increased serial dependence when working memory demands were high. Considering that the cartoon faces were on the screen, this may indicate competition between internal and external attention due to the dual-task demands, which impaired the ability to maintain the second face more when three as compared to one cartoon face were displayed on the screen (Baddeley, 2003; Bae & Luck, 2019; Manza et al., 2014; Riley & Constantinidis, 2016; van Ede, 2018; Yoon et al., 2006). Together, the EEG results indicate that stimulus uncertainty for the second face increased over time from early perceptual to working memory stages due to high perceptual and working memory demands, leading to greater reliance on the first face and so contributing to serial dependence.

Overall, Paper III shows that perceptual and working memory processing demands separately influence serial dependence in facial identity and that neural mechanisms operating on different time scales for a previous and current face contribute in part jointly and independently to serial dependence. This suggests a role for both perception and working memory in the manifestation of serial dependence in facial identity.

General discussion

The overarching aim of this thesis is to advance the understanding of how perceptual and working memory processes contribute to serial dependence in facial identity. In the following sections, I first separately discuss the evidence supporting the involvement of perceptual and working memory processes, followed by a discussion of the evidence supporting the interaction between the two in terms of their contribution to serial dependence in facial identity. Finally, I discuss the strengths and weaknesses of this thesis as well as suggestions for future developments in the study of serial dependence in facial identity.

Serial dependence and perception

In the three papers that are part of this thesis, I consistently show that serial dependence in facial identity can occur even when a previous face is merely perceived and explicitly categorized as irrelevant to a current task. This contrasts with findings showing that serial dependence for non-facial objects and features depends on whether a stimulus was relevant to the previous task and intentionally memorized or used in a decision process (Bae & Luck, 2020; Ceylan & Pascucci, 2023; Czoschke et al., 2019; Houborg et al., 2023a, 2023b; Pascucci et al., 2019; Pascucci & Plomp, 2021). The present results support face superiority in visual processing (e.g., Palermo & Rhodes, 2007) and the studies of Turbett et al. (2019; 2021; 2022a; 2022b), in which the previous face was also a no-response face. However, it was not the aim of Turbett et al. to investigate whether serial dependence occurs independently of task-relevance, so this was not explicitly tested. In Paper I, I specifically tested whether serial dependence was due to the response or the stimuli of the previous trial rather than the no-response face within the same trial. I did not detect serial dependence from the response in the previous trial, suggesting that the effect was due to the no-response face within the same trial. Another difference between the studies in this thesis and the Turbett et al. studies is that participants in Turbett et al. were familiarized with the faces and provided with autobiographical information such as names and family relations, which may have activated associative networks during recognition (Young & Bruce, 2023). In the three papers that are part of this thesis, the faces were unfamiliar to encourage participants to rely on visual rather than autobiographical information. The results

of this thesis therefore provide evidence that a previously seen unfamiliar face that is merely perceived can still induce serial dependence.

That the perception of a face is sufficient to induce serial dependence also supports previous findings showing that age-related information from faces is continuously integrated over time, causing an altered perceptual experience (Manassi & Whitney, 2022). However, it cannot be completely ruled out that this ‘perceptual’ effect does not occur for non-facial objects and features, as serial dependence in numerosity judgments has been shown to occur without an explicit response to a previous stimulus (Fornaciai & Park, 2018a). Similar to faces, numerosity judgments involve a complex stimulus that may activate multiple perceptual and cognitive processes in the brain (Harvey, 2016). This indicates that the extent to which a stimulus is processed determine the serial dependence effect, consistent with notions of the role of attention in serial dependence (Fischer & Whitney, 2014; Fornaciai & Park, 2018b; Fu & Mei, 2024; Kim et al., 2020; Liberman et al., 2016; Manassi et al., 2018; Rafiei et al., 2021).

It has been suggested that higher-order decision processes actively monitor the flow of sensory information and selectively integrate only information that was relevant to a previous decision (Feigin et al., 2021). The finding that serial dependence was induced by a task-irrelevant face may not necessarily challenge this view. Faces are inherently behaviorally relevant stimuli, and we can extract a lot of information from a person’s face (Dobs et al., 2019; Palermo & Rhodes, 2007). In particular, the processing of facial expressions can facilitate the recognition of danger and is useful for responding appropriately in threatening situations (LeDoux, 1996) and is thought to occur rapidly partially outside of conscious awareness (Longin et al., 2013; Phelps & LeDoux, 2005). The faces used in all three papers in this thesis showed ‘neutral’ expressions. However, faces are emotionally meaningful stimuli regardless of expression, and identity and expression recognition do not necessarily occur independently (Palermo & Rhodes, 2007; Rhodes et al., 2015, Sutherland et al., 2020). Indeed, it has been shown that serial dependence in emotional expression is mediated by the similarity of facial identities (Liberman et al., 2018). Mere attention to a face may therefore automatically activate decision processes, which makes it a relevant stimulus independent of task instructions. In addition, serial dependence is known to be sensitive to stimulus uncertainty (Cicchini et al., 2018; Kim & Alais, 2021; van Bergen & Jehee, 2019), and task instructions such as categorizing a stimulus as task-irrelevant may reduce uncertainty for that stimulus (Frings et al., 2019). Alternatively, but not necessarily exclusively, the first face, that was categorized as task-irrelevant, may have been considered less uncertain as compared to the second task-relevant face, which may have contributed to serial dependence in line with Bayesian and predictive coding theories (e.g., Friston, 2005; Ma et al., 2023). This could indicate that the serial dependence effects obtained from the mere ‘perception’ of a previous face in my experimental work are not completely independent of task instructions and decision processes.

Paper I examined the time course of serial dependence in order to determine how serial dependence manifests over time from perceptual to working memory stages. Previous findings investigating the temporal dynamics of serial dependence in spatial position, using the same response delays as in Experiment 1, Paper 1, suggest that serial dependence does not act directly on the perception of a second stimulus (Bliss et al., 2017). In particular, Bliss et al., observed a repulsive effect for judgments of spatial position with a response delay of 0 s, consistent with Experiment 1, which also showed a trend towards a repulsive effect with a 0 s response delay. However, this does not decisively rule out the possibility that serial dependence acts on the perception of a subsequent face. The fact that no serial dependence was obtained at a response delay of 0 s could be due to perceptual interference from the adjustment face (Di Lollo & Dixon, 1988), as no noise masks were used in the present experimental work. Furthermore, the duration of iconic memory may depend on the stimulus, and prolonged duration of iconic memory may manifest due to the complexity of the stimulus (Rensink, 2014). Given the high complexity of faces (Bruce & Young, 2023; Sheehan & Nachman, 2014), a delay of 1 s may reflect at least some residual iconic memory traces, which would support the notion of serial dependence emerging during perceptual processing of a subsequent face. However, serial dependence in orientation has been shown to manifest at a response delay of 0 s when stimulus uncertainty was manipulated and more attention was allocated to the stimulus (Manassi et al., 2018). This makes it possible that the effect of response delay on serial dependence and whether the effect manifests during the perception of a subsequent stimulus depends to some extent on stimulus uncertainty and attention.

That serial dependence is directly linked to the perception of a subsequent face is confirmed by the EEG results in Paper III. In Paper III, I manipulated perceptual demands by superimposing a scene image with low or high transparency on the faces, as serial dependence has been shown to manifest more strongly with increased sensory processing of stimuli (Manassi et al., 2018). Accordingly, serial dependence was more pronounced at high as compared to low perceptual demand. However, no relations between serial dependence and the P200 ERP were obtained, suggesting that increased sensory processing *per se* (Bankó et al., 2011) may not be underlying serial dependence in facial identity. The first ERP for the second face identified in the exploratory analyses was within a time window and had a similar topography to the N250r ERP (Andrews et al., 2017; Schweinberger & Neumann, 2016) and was reduced at high perceptual demand, when serial dependence was most pronounced. It is thought that perceptual processing capacity is limited and proceeds automatically and in parallel on all stimuli within its capacity (Eayrs & Lavie, 2018; Lavie et al., 2003). The N250r has previously been associated with capacity limitations in perceptual face processing showing a reduced response when processing capacity is depleted (Neumann & Schweinberger, 2009). So, more extensive processing of the scene that was more visible at high as compared to low perceptual demand may have depleted perception, leaving less capacity for

processing the second face, which increased serial dependence, consistent with serial dependence being sensitive to stimulus uncertainty (Cicchini et al., 2018; Kim & Alais, 2021; van Bergen & Jehee, 2019). This result also suggests that serial dependence in facial identity relies to some extent on the same mechanisms as other temporal context effects, such as repetition priming, as the N250r is known to be sensitive to repetition priming effects for faces (Schweinberger & Neumann, 2016).

Further evidence that perceptual processing plays a role in serial dependence is that individual differences in N170 amplitude for the second face in Paper III were associated with the magnitude of serial dependence. This suggests that when structural encoding and the ability to extract and accumulate information necessary for recognition from the second face was impaired (Bankó et al., 2011; Jemel et al., 2003, Piliastides et al., 2006; Rousselet et al., 2008; Sreenivasan et al., 2009) serial dependence was more pronounced. This provides further evidence that stimulus uncertainty plays a role in serial dependence and suggests that serial dependence is, at least to some extent, related to structural encoding of faces (Bentin & Deouell, 2000). This result may further suggest that individual differences in perceptual capacity (Eayrs & Lavie, 2018; Ward, 2019) are related to serial dependence and may be captured at early stages of face processing, corresponding to the N170 time window. Overall, these ERP results of Paper III are consistent with the notions of Bayesian and predictive coding theories, which state that more weight is given to previous sensory information when the current sensory input is uncertain (e.g., Friston, 2005, Ma et al., 2023).

In Paper II, the two consecutive faces were processed under variations in concurrent working memory load and serial dependence was most pronounced at high working memory load. The ERP results showed that individual differences in N170 amplitude for the first face due to variations in working memory load predicted serial dependence independent of working memory capacity; participants who exhibited stronger serial dependence showed larger amplitude differences between working memory load conditions than those who exhibited weaker serial dependence. This may indicate that participants for whom serial dependence was more pronounced, attentional selection at high working memory load was impaired, thereby facilitating unintentional maintenance of this face in working memory. Conversely, participants for whom serial dependence was less pronounced may have been better able at preventing the first face from being encoded in working memory regardless of working memory load. However, working memory capacity is thought to be closely linked to attentional selection mechanisms (Unsworth, 2016), which may challenge this interpretation.

In Paper II, the cartoon faces that functioned as working memory load were presented before the first face, thereby suggesting an alternative explanation for the relationship between serial dependence and the N170 effect obtained. Sensory traces of previously encoded objects can persist over time and act as sensory load, leading to sensory uncertainty regarding a subsequently processed stimulus (Grill-Spector

et al., 2006; Guo et al., 2021; Landman et al., 2003; Mongillo et al., 2008; Sligte et al., 2008; Stokes, 2015; Vandenbroucke et al., 2014). So, as a result of individual differences in perceptual capacity (Eayrs & Lavie, 2018; Ward, 2019), it is possible that for some participants structural encoding of the first face was impaired regardless of working memory load, which prevented serial dependence from taking full effect. Individual differences in serial dependence in facial identity have been shown to occur particularly when stimulus uncertainty for a previous face is high due to external noise and has been attributed to a “general response bias” related to subjective confidence and internal or external decision processes (Kim & Alais, 2021). Alternatively, but not exclusively, the present result may confirm that reduced confidence related to an internal decision about a previous face due to impaired sensory input can prevent serial dependence, as it has been shown that serial dependence is reduced when less confidence is reported in relation to a previous stimulus (Samaha et al., 2019). However, as I did not collect subjective confidence ratings, this is purely speculative. Nevertheless, this result suggests that structural encoding (Bentin & Deouell, 2000) also for a previous face plays a role in serial dependence in facial identity and may further suggest that perceptual capacity also for a previous face can modulate serial dependence. This further support Bayesian and predictive coding theories of perception and that less weight is given to previous unreliable sensory input, preventing them from influencing the processing of subsequent stimuli (e.g., Friston, 2005; Ma et al., 2023).

Further evidence for a link between perceptual processing of a previous face and serial dependence may be provided in Paper III, in which exploratory EEG analysis identified a later ERP effect in relation to the first face that predicted serial dependence. This ERP manifested within a time window and topography similar to the FN400 ERP, which typically shows a more negative amplitude in response to unfamiliar than to familiar stimuli (Bader et al., 2010; Bridger et al., 2012), and showed an amplified amplitude at high perceptual demand, where serial dependence was most pronounced. It may seem contradictory to attribute the mechanism underlying this ERP to familiarity, as the faces used in this thesis were not familiar. However, familiarity is influenced by multiple factors, such as relative familiarity, which results from repeated exposure to an event within an experimental setting, and pre-experimental baseline familiarity, which refers to exposure outside the experimental setting (Bader et al., 2010). It is therefore possible that faces that were processed at high perceptual demand, which were less visible, were recognized and perceived as less familiar than faces processed at low perceptual demand, which can be attributed to a pre-experimental effect of baseline familiarity. Unfamiliar stimuli are processed to a greater extent than familiar stimuli (Manahova et al., 2018), which may indicate that more attention was allocated to processing the first face at high perceptual demand, leaving fewer resources for stimulus suppression. Considering serial dependence was most pronounced at high perceptual demand could imply that impaired stimulus inhibition due to attentional competition facilitated the encoding of the first task-irrelevant face in working memory, subsequently influencing the

processing of the second face. However, an alternative explanation for this ERP in the context of working memory is provided in the next section.

Regardless, the results presented in this thesis suggest that face-specific processing and perceptual mechanisms plays an important role in serial dependence in facial identity.

Serial dependence and working memory

All three papers that are part of this thesis consistently show that working memory plays a role in serial dependence. In Paper I, no serial dependence was obtained from the previous trial's stimuli or response in any of the experiments. As two faces were presented within the same trial, this may reflect the capacity of working memory for faces, which is thought to be limited to a maximum of one to two faces (Alvarez & Cavanagh, 2004; Curby & Gauthier, 2007; Eng et al., 2005), and that stimulus information from the previous trial was removed from working memory to release capacity for the stimuli in the next trial. Paper I also showed that prolonged maintenance of the second face leads to increased serial dependence, possibly indicating that the memory representation of the second face integrated with the previous face over time. Although the precise temporal dynamics of serial dependence in facial identity differed from that previously identified for spatial position (Bliss et al., 2017), the observation at the 6 s response delay is similar, suggesting that working memory contributes to serial dependence regardless of stimulus type.

As discussed in the previous section, serial dependence in Paper I may have occurred during the perception of the second face, making it possible that the effect persisted for up to 6 s and increased during the maintenance of this face in working memory. The reactivated memory representation of the target stimulus of the previous trial and the altered representation of a current stimulus as a result of serial dependence may indeed persist for a considerable period of time (Bae & Luck, 2019; Fornaciai & Park, 2020). In addition, uncertainty in working memory is thought to be continuously estimated and maintained (Bays, 2014; Bays et al., 2024; Li et al., 2021) and resolution may be a particularly adaptive property of working memory for faces. Reevaluating the results of Paper I, it is possible that serial dependence persisted because the internal noise increased with prolonged maintenance of the second face in working memory and impaired the memory resolution of the second face (Ma et al., 2014), leading to internal stimulus uncertainty and greater reliance on the first face. According to models of attractor dynamics in working memory, the memory representation of a current stimulus may shift towards stable neural states and local attractors, reflected as recently experienced stimuli, when the memory of the current stimulus deteriorates due to prolonged working memory

maintenance (Barbosa et al., 2020; Pascucci et al., 2019). However, although working memory representations for faces have been shown to decay from 1 to 6 s, the duration of the maintenance phase appears to influence memory retrieval but not memory resolution (Krill et al., 2018). It is therefore possible that in Paper I, deficits in accessing the memory of the second face with prolonged maintenance are what underlie stimulus uncertainty and the serial dependence effects obtained at the 6 s response delay.

In Paper I, for a response delay of 3 s, no significant serial dependence was obtained, which raises the question of whether serial dependence could act directly on the perception of the second face and then persist over time. In this case, the temporal dynamics of serial dependence were the same regardless of whether the first face was merely attended to or actively maintained until the adjustment response, suggesting that the temporal dynamics obtained in Paper I may be a particular preventative property of serial dependence in facial identity. There is evidence that there is a time window of ~ 3 s in which representations in working memory are fragile, yet highly precise, and can be easily overwritten (Sligte et al., 2008, 2010). If serial dependence arises from memory traces of previous stimuli, the effect would be eliminated when these traces are no longer accessible. It is therefore possible that at a response delay of 3 s, the first face was overwritten by the second face, regardless of whether this face was maintained in working memory unintentionally or actively, preventing serial dependence from taking full effect. So, it appears that attractor models or working memory for faces cannot explain the lack of serial dependence for the 3 s response delay and the temporal dynamics obtained in Paper I.

Experiment 2, Paper I, helped clarify the difference between serial dependence and serial effects resulting from interactions within working memory. The results showed that the serial effect obtained when a face was presented after rather than before the response face exhibited different temporal dynamics, with an effect that decreased somewhat linearly over time, consistent with a decay in working memory for faces from 1 to 6 s (Krill et al., 2018), whereas serial dependence from the first face on responses to the second face appeared in a curvilinear fashion. The parametric and nonparametric results were not consistent when responding to the first face, as the DoG analysis showed no significant serial effects, while the nonparametric analysis showed significant effects at response delays of 1 and 3 s. Bae and Luck (2017) found that working memory interactions showed a pattern opposite to serial dependence, such that similar orientations were repelled by each other, while dissimilar orientations were assimilated. As noted under the heading “Statistical analyses of serial dependence”, the DoG fails to capture repulsive effects between dissimilar stimuli (Bliss et al., 2017), so it is possible that this function is sensitive to stimulus differences overall and did not properly capture the serial effects that resulted from working memory interactions.

Bae and Luck (2017) suggested that the difference between serial dependence and working memory interactions may be that the presentation of two similar sequential stimuli within the same trial may promote comparison between them to actively separate them, leading to repulsive effects, which would not be necessary when serial dependence is assessed between trials. This is supported by findings showing that perceptual comparisons of similar orientations lead to a repulsive effect, whereas perceptual decisions lead to serial dependence (Fritsche et al., 2017). Active separation by comparison is not consistent with the results of Paper I, as serial dependence between similar faces was obtained even though the faces were presented within the same trial. Reevaluating the results, similar effects of response delays to the serial effects induced by working memory interactions in Experiment 2, Paper I has been shown for facial identity and location binding in working memory (Spotorno et al., 2018). This may suggest that the serial effects emerged from binding between the second and firstly presented face and that the temporal dynamics obtained simply reflect the duration of binding effects in working memory that are distinct from those of serial dependence.

In Paper II, I provided additional evidence for the contribution of working memory processes to serial dependence and showed that working memory capacity is a strong predictor of serial dependence when task demands increase, explaining 40 % of the variance. Participants with low working memory capacity showed serial dependence regardless of working memory load, while participants with high working memory capacity only showed serial dependence when working memory load was high. Previous studies based on piecemeal experimental work have not found a direct relationship between working memory capacity and serial dependence (Bansal et al., 2023; Zhang & Whitney, 2017). Dual-task experiments have the potential to shed light on how working memory functions under increased processing demands and may sometimes be required to determine the exact nature of the relationship between working memory capacity and performance on visual tasks (Doherty et al., 2019; Redden et al., 2023). The results in Paper II are indeed consistent with previous findings showing that dual-task designs and concurrent working memory load have a modulating effect on serial dependence in orientation judgments (Markov et al., 2024). The results of Markov et al. were mainly explained in the context of attractor models of working memory, in which memory for the current stimulus may have deteriorated with increasing concurrent load and therefore shifted towards stable neural states represented by recent stimulus events (Barbosa et al., 2020; Pascucci et al., 2019).

In Paper II, EEG was used to investigate the neural mechanisms associated with working memory that contributed to the serial dependence effects obtained, which do not support the explanation of Markov et al. Rather, these results suggest that neural mechanisms associated with working memory maintenance and the ability to selectively suppress the first face played an important role in serial dependence. Working memory capacity is closely related to the ability to selectively decide

which information is relevant or irrelevant, regardless of whether this information is maintained in working memory or encountered externally (Engle, 2002; Engle & Kane, 2004; Vogel et al., 2005; Ye et al., 2018). It is thought that external suppression and internal removal of information from working memory rely on the same attentional selection mechanisms and require more capacity than remembering an item and selectively encoding task-relevant stimuli (Aron et al., 2003; Aron & Poldrack, 2006; Aron et al., 2004; Cheng et al., 2012; Fawcett et al., 2013; Wang et al., 2019). In Paper II, participants with high working memory capacity showed significant differences in NSW amplitude between high and low working memory load, whereas participants with low working memory capacity showed no difference in NSW amplitude between working memory load conditions. Individual differences in NSW amplitude between working memory load conditions were also a significant predictor of serial dependence, explaining 26 % of the variance. This suggests that serial dependence was, at least to some extent, due to impaired attentional selection mechanisms at high working memory load, which facilitated unintentional maintenance of the first face in working memory and subsequently influenced processing of the second face. In addition, the behavioral results suggest that participants with high working memory capacity were better able to selectively maintain or retrieve the second face than participants with low working memory capacity, as working memory capacity was a significant predictor of adjustment errors, such that participants with high working memory capacity showed smaller adjustment errors.

Whether and how the results of Paper II can be generalized to those of Markov et al. and other stimuli is unclear due to differences in experimental design and stimuli. However, I found no evidence that the relationship between working memory capacity and serial dependence was specifically related to working memory for faces, as no difference in serial dependence was obtained between upright and inverted cartoon faces. This was likely due to featural rather than holistic processing of the cartoon faces because of their distinct facial features, suggesting that the maintenance of non-facial objects in working memory may also modulate serial dependence in facial identity.

In Paper III, serial dependence manifested more strongly at high as compared to low perceptual and working memory demand and exploratory EEG analysis identified several ERP components related to working memory processing. Although the ERPs were not triggered by working memory demands *per se*, some of them may best be interpreted as related to working memory processes, such as greater frontal negativity at high as compared to low perceptual demand ~ 400 ms after the onset of the first face. As noted in the previous section and in line with Bader et al. (2010) and Bridger et al. (2012), this ERP may be interpreted as reflecting a familiarity effect. However, frontal negativity with a similar topography and time window is also observed in relation to forget cues in I-MDF experiments, in which participants are post-cued to forget an item after encoding, and is generally interpreted as

impaired inhibitory mechanisms, as it is associated with reduced forgetting (Alfonso & Menor, 2021; Kissler & Hauswald, 2022; Hauswald et al., 2011). Participants were instructed to attend to the first face while being informed that this face was irrelevant to the adjustment task and therefore unable to suppress this face by withdrawing their attention, which may have activated similar inhibitory mechanisms as in I-MDF experiments. Serial dependence was most pronounced at high perceptual demand, and stimuli that are less visible require more attention to extract relevant sensory information from noise and optimal working memory performance depends on effectively filtering out irrelevant information at early stages of perceptual processing (Carrasco, 2011; Sreenivasan et al., 2009; Zanto & Gazzaley, 2009). It is therefore possible that processing the first face required increased attention when perceptual demand was high, leaving fewer resources available for stimulus inhibition, facilitating unintentional maintenance of this face in working memory, subsequently influencing processing of the second face, contributing to serial dependence. This interpretation is supported by the second ERP for the first face in Paper III, which predicted serial dependence and had a similar topography to the NSW in Paper II, reflecting unintentional maintenance of the task-irrelevant face in working memory. This interpretation applies regardless of whether the first ERP effect for the first face in Paper III reflects inhibitory mechanisms or a familiarity effect, as both indicate competition between stimulus suppression and stimulus processing.

For the second face, Paper III reports an ERP manifesting as greater left parieto-occipital negativity at high as compared to low perceptual demand, for which serial dependence was more pronounced, ~600 ms after stimulus onset. Greater negativity within this time window and topography is consistent with ERP activity elicited in response to remember cues in I-MDF experiments, presumably reflecting impaired selective rehearsal of task-relevant information (Alfonso & Menor, 2021; Kissler & Hauswald, 2022). In addition, impaired recollection, which refers to retrieval of the physical features of a studied item, is associated with greater negativity within this time window and topography (Sun et al., 2024). This may suggest that selective rehearsal or recollection was impaired when the second face was processed at high perceptual demand, leading to internal stimulus uncertainty (Bays, 2014; Bays et al., 2024; Li et al., 2021) and therefore greater dependence on the first face.

In Paper III, a third ERP associated with serial dependence manifested as greater right-fronto-central negativity at high as compared to low perceptual demand ~1,000 ms after the onset of the second face. This ERP is consistent with those observed for post-retrieval monitoring, which refers to monitoring the information of memory retrieval considering current behavioral goals (Norman & Borrow, 1979), with more negative amplitudes thought to reflect impaired monitoring as they are associated with incorrect stimulus judgments (Wilding & Rugg, 1996). Post-retrieval monitoring is influenced by the quality of information available to assess a memory, and subjective confidence in whether retrieval was successful may be

reduced if the information obtained from a retrieval attempt is inadequate (Henson et al., 2000; Henson et al., 1999; Rugg et al., 2000). It is therefore possible that when the second face was processed at high perceptual demand for which serial dependence was most pronounced, post-retrieval monitoring was impaired, which in turn affected participants' confidence regarding successful retrieval of this face and caused greater dependence on the first face. Subjective confidence has previously been associated with serial dependence (Maldonado Moscoso et al., 2023; Samaha et al., 2019; Suárez-Pinilla et al., 2018), and reduced confidence in the judgment of a current stimulus has been shown to lead to stronger serial dependence (Suárez-Pinilla et al., 2018). However, as mentioned in the previous section, subjective confidence ratings were not collected, meaning this is purely speculative.

The second and third ERPs related to the second face in Paper III were positively associated, which may suggest that impairment in selective rehearsal or recollection caused impairment in post-retrieval monitoring and contributed jointly to serial dependence. Indeed, recollection and post-retrieval monitoring have been shown to covary (Hamaya et al., 2008), making this the most likely explanation for the second and third ERPs and their association in terms of contribution to serial dependence. Considering that the time window of the third ERP with respect to the second face in Paper III corresponds to the response delay of 1 s in Paper I, it is worth considering that serial dependence at this response delay may be due to post-retrieval working memory rather than perceptual processes. However, this cannot be clearly established due to differences in experimental designs in Papers I and III.

Regarding Paper III, I observed greater attenuation of frontal alpha power at high as compared to low working memory demand, which was predictive of serial dependence. This alpha attenuation was observed during the encoding phase of the cartoon face(s), which occurred during the maintenance period of the second face. The introduction of a secondary task is known to interfere with ongoing working memory maintenance (Baddeley, 2003; Yoon et al., 2006), resulting in less accurate memory representations due to shifts in external and internal attentional focus (Bae & Luck, 2019). This may suggest that serial dependence increased because more attention was required for external processing at high as compared to low working memory demand, resulting in fewer resources being available to maintain the second face, increasing stimulus uncertainty (Bays, 2014; Bays et al., 2024; Li et al., 2021), causing greater dependence on the first face. In addition, attenuation of frontal alpha power is associated with reduced top-down control processes that protect information maintained in posterior sensory regions from interference (van Ede, 2018). In this regard, interference from the first face could be greater if protective mechanisms failed to function properly, as more attention was required to process three as compared to one cartoon face, leading to stronger serial dependence effects. Regardless, this result confirms the results of Paper II, showing that serial dependence is mediated by task demands. Overall, the suggested working

memory mechanisms related to the second face in Paper III are consistent with the notion that serial dependence is more pronounced when internal stimulus information is uncertain (Bays, 2014; Bays et al., 2024; Li et al., 2021) because less weight is given to unreliable stimulus information, leading to greater reliance on previous stimulus information (e.g., Cicchini et al., 2018; Friston, 2005; Ma et al., 2023). Taken altogether, the results presented in the present thesis provide strong evidence that working memory mechanisms contribute to serial dependence in facial identity.

Serial dependence and the interaction between perception and working memory

The previous two sections suggest that both perceptual and working memory processes contribute to serial dependence. Although Paper III reports no interaction between perceptual and working memory demands, this does not rule out the possibility that perceptual and working memory processes do not interact in their contribution to serial dependence. Rather, the collective results suggest that serial dependence was due to unintentional maintenance of a previous face that was merely perceived in working memory, which influenced processing of a subsequent face. This was confirmed by the NSW observed in Papers II and III as the NSW is thought to reflect information that is maintained in working memory (Ruchkin et al., 1995). The results of Experiment 1, Paper I showed that serial dependence only occurred at an ISI of 1 s, supporting the notion that the visual environment is expected to be stable within short temporal delays (Burr & Cicchini, 2014; Cicchini et al., 2018). These results are consistent with other temporal context effects such as repetition priming, where priming effects for unfamiliar faces have been found most consistently within short temporal intervals (Bentin & Moscovitch, 1988). This may be related to findings showing that working memory representations of facial identity remain active for ~ 1 s before entering a state of activity silence, possibly because facial identity is a stable attribute that does not need to be continuously updated during working memory maintenance (Bae, 2020). However, it is unclear whether this also applies to facial identities that are unintentionally maintained. Nevertheless, the identity of faces should remain stable over brief periods of time, and serial dependence may therefore reflect a phenomenon that promotes this stability by reducing random fluctuations that would otherwise impair facial recognition. The present thesis provides evidence that the interplay between face perception and working memory plays a role in stabilizing facial identity judgments.

The results of Papers II and III provide further evidence for an interaction between perceptual processing of faces and working memory in terms of their contribution

to serial dependence. In Paper II, the effect of working memory load on perceptual processing of the first face contributed significantly to serial dependence, possibly due to individual differences in perceptual capacity (Eayrs & Lavie, 2018; Ward, 2019), consistent with the notion that information maintained in working memory can influence how an object is perceived (Grill-Spector et al., 2006; Mongillo et al., 2008; Stokes, 2015; Teng & Kravitz, 2019). Moreover, the N170 effect due to variations in perceptual demand for the second face in Paper III was a strong predictor of the second ERP obtained for the same face, which was interpreted as reflecting recollection (Sun et al., 2024), which in turn affected post-retrieval monitoring (Henson et al., 2000; Henson et al., 1999; Rugg et al., 2000), both of which are properties of working memory. This suggests a link between early structural encoding of faces and extraction and information accumulation during perception (Bentin & Deouell, 2000; Philiastides et al., 2006; Rousselet et al., 2008) and working memory processing in terms of their contribution to serial dependence and supports a disruption of working memory function when perceptual input is less clear (Santana et al., 2013). Paper III further indicates that the memory representation of the second face may have been impaired due to competition between internal working memory maintenance and external perceptual stimulus processing as reflected in attenuation of alpha power (Baddeley, 2003; Bae & Luck, 2019; Manza et al., 2014; Riley & Constantinidis, 2016; van Ede, 2018; Yoon et al., 2006), further supporting an interplay between working memory and perceptual processing in terms of their contribution to serial dependence. So, the answer to the question of whether perceptual and working memory processes interact in terms of their contribution to serial dependence in facial identity appears to be: Yes, they do.

Strengths, weaknesses and future developments

Strengths and weaknesses

One factor that is relevant to all three papers in this thesis is the stimulus distribution used. The faces in the morphed continuum were overall very similar, and discrimination between similar faces is more difficult as compared to simpler objects (Biederman & Kalocsai, 1997), which may lead to swapping errors and false serial effects in working memory tasks (Almeida et al., 2015). Another factor, also related to the stimuli used, is that studying perception and recognition of unfamiliar faces is challenging because it is difficult to control the strategies that participants use in memory and recognition tasks that involve faces. Participants often use a strategy in which they name the faces, which means that their memory and recognition is partly based on autobiographical and not just visual information. For example, one participant assumed it was a continuum of three faces and formed three families with different surnames. This also means that this participant gave a categorical response that influenced the sensitivity of the adjustment response.

Similarly, one participant named the cartoon faces after their classmates, which may also affect the way they were encoded and remembered.

Another factor that applies to all three papers is the fact that no noise masks were used between the presentation of the stimuli. As mentioned earlier, this may have resulted, for example, in the adjustment face masking the second face at the 0 s response delay in Experiment 1, Paper I. The reason for not using noise masks was twofold. The precise mechanisms of visual masking remain largely unknown, and I also wanted to avoid interference between the mask and the facial images, which may have influenced the perception of the faces (Bachmann & Francis, 2014; Eriksen, 1980). Another factor related to the experimental task that could perhaps be considered a weakness is the fact that participants were informed about the task-irrelevance of the first face, which is usually not the case in serial dependence experiments. However, this may be interpreted as a strength rather than a weakness. In reality, we often see numerous faces passing by one after the other, but we do not usually memorize and reproduce every face we encounter. Therefore, this experimental procedure may be more reflective of how serial dependence operates in reality, for example in legal contexts such as eye-witness testimonies and lineups where facial images are sometimes viewed sequentially prior to identification.

Other factors that may limit the interpretation of the results relate to the statistical analyses. First, the amount of data in Experiment 1, Paper I, may not have been sufficient to draw reliable conclusions using frequentist statistical methods. Previous findings have shown that serial dependence typically extends over a time span of ~ 15 s back in time (Manassi & Whitney, 2024), whereas the results of Experiment 1 only showed serial dependence at an ISI of 1 s and not for longer ISIs. Second, the categorical analysis in Papers I and II does not take into account the sensitivity of the adjustment response. In addition, by using an exploratory analysis for the EEG data in Paper III, I was unable to determine the exact underlying mechanisms of the EEG effects, which somewhat limits the conclusions. However, the use of an exploratory analysis and EEG is also a strength as it has a high temporal resolution that allowed me to determine the precise time windows in the EEG data that were predictive of serial dependence. This contributes to the understanding of how serial dependence operates over time across a preceding and subsequent face and from early perception to memory-related processing. The proposed underlying mechanism identified in the exploratory analysis also opens several avenues for further studies on the neural mechanisms underlying serial dependence in facial identity. In addition, the use of EEG strengthens previous behavioral findings, which suggest that face-specific processes are involved in serial dependence effects by targeting ERPs known to respond specifically to faces.

Future developments

The papers comprising the present thesis extend knowledge of how perceptual and working memory processes contribute to serial dependence in facial identity.

Whether the results presented in this thesis can be applied to realistic situations requires further investigation. The investigation of serial dependence on object features such as shape has been extended to clinical images and radiographs (Manassi et al., 2019; Manassi et al., 2021; Ren et al., 2023a, 2023b), demonstrating that this phenomenon manifests in more realistic stimulus judgments. Regarding faces, it may be beneficial for future studies to investigate whether serial dependence in facial identity manifests in eye-witness testimonies such as lineup procedures. In lineups, facial images are viewed either sequentially or simultaneously, and the so-called ‘fillers’ (i.e., innocent people in police lineups) are selected to resemble the offender to avoid drawing unnecessary attention to the offender and facilitating false identifications. As serial dependence is known to occur primarily between similar faces, it is of interest to understand whether this phenomenon is relevant in such contexts. The use of video footage and virtual reality may be beneficial in further studies of serial dependence in facial identity to determine the precise extent to which the effect arises in dynamic contexts.

To further determine how and whether serial dependence is related to facial recognition, it would be beneficial to examine this phenomenon in the context of norm-based coding and face-space (Valentine, 1991; Valentine et al., 2016). Adaptation effects for facial identity, which is a phenomenon opposite to serial dependence, are known to benefit facial recognition, and the extensive study of adaptation effects has supported the notion of norm-based coding of faces (Rhodes et al., 2014; Webster, 2015). Adaptation effects for facial identity have been shown to recalibrate face-space and the norm face may be altered based on short-term experience of faces (Van Rensbergen & Op de Beeck, 2013). It remains largely unknown how and whether serial dependence influences or is influenced by norm-based coding and face-space. Further investigation into whether serial dependence is related to norm-based coding as a counterpart to adaptation effects will advance understanding not only of serial dependence but also facial recognition. To further investigate how serial dependence operates in face perception and recognition, eye tracking may also provide a useful technique to determine whether serial dependence is related to the processing strategy used at encoding and recognition (i.e., holistic and feature-based) of faces.

Conclusion

How the past influences what we see has been a topic of interest for several decades, dating back at least to the 19th century and the work of von Helmholtz. The past can influence perceptual judgments in various ways, which can be beneficial or detrimental depending on the context and stimulus. The goal of perception is to obtain accurate information about objects and events in the world in order to guide our thoughts and actions. The perception of a stable visual world forms the

foundation on which other visual functions are based, allowing us to judge the positions and movements of our own body as well as other objects and people (Bridgeman, 2010). Serial dependence may achieve this stability by actively smoothing the appearance of objects across brief temporal delays, with the specific computational goal of stabilizing perception, memory, and decisions, including judgments of facial identity. The present thesis contributes to the understanding of the mechanisms underlying serial dependence in facial identity, showing how perceptual and working memory mechanisms independently and jointly contribute to this phenomenon. However, some readers may think that one question remains unanswered: Is there a specific neural signature of serial dependence in facial identity in the brain? The present thesis did not aim to determine this but rather sought to understand how known cognitive and sensory processes contribute to serial dependence in facial identity. Perhaps serial dependence in facial identity is a by-product of an interaction between multiple cognitive and sensory processes, or perhaps the neural signature of serial dependence is so subtle that it is overshadowed by other, parallel neural processes. Faces are behaviorally relevant and most of us see a continuous stream of faces every day. The results of the present thesis bring us one step closer to understanding how perception and working memory work together and independently to process the constant stream of sensory information in our lives.

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