TEMPORAL STRUCTURES IN PERCEPTION AND ATTENTION

DISSERTATION
submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy in Neuroscience

Irene Echeverria Altuna

Green Templeton College
University of Oxford

Oxford, June 2024

Acknowledgements

Over the past four years, I have drifted away from a linear conception of time and towards an understanding of the dynamically changing interdependencies between past, present, and future. I have learned that while the content of memories is about the past, their function is serving the present and the future. The work in the present thesis is, therefore, the result of interactions between my circumstances over the past years and the extraordinary people that populate my memories, from the oldest to the most recent.

For this and countless other lessons which I will continue to uncover and cherish in the years to come, I thank Kia Nobre. I owe the decent parts of this thesis to your unique combination of deeply rooted knowledge, sagacious intuition, mind-bending clarity of thought, and generous mentorship. I am also infinitely grateful to my other supervisors: Kate Watkins and Kerry Walker. Kate, your kindness, guidance, and support have been unmatched. Thank you for welcoming me into your group with open arms, patiently guiding me through the steep hill of fMRI analyses and mentoring me by example. Kerry, my first memories of auditory research are happy, thanks to you. I look forward to many more to come.

Sage, you have been a role model to me in more ways than I can convey. My appreciation of your clever and helpful insights in lab meetings has evolved into a profound admiration of your academic brilliance, boundless creativity, infinite generosity, and relentless efforts to turn the Brain and Cognition Lab into a community which has wrapped me in self-confidence and unending fun. The members of this community have engrained themselves into me and they have immensely improved this thesis. Thank you for the endless companionship, generosity, scholarship, and joy to Dani, Freek, Dejan, Nir, Oli, Andrew, Gwen, Levi, Rhianna, Anna, Sarah, Lauren, Katharina, Oscar, Joel, Nahid, Mats, Chet, Alessandro, Jemma, Bo, Joey, Marcus, Sammi, Anne, Arden, Tiago, Pearl, Cara, Lizzie, Dongyu, Meadhbh, Jasper, Giedre, Oana, and Noam. A special thanks goes to Lola and Amelia for making EEG/MEG preparation time fly by. The B&C has taught me the wonders of shared learning. My thanks also go to the members of the Brain, Speech, and Language Lab, including Birtan, Nilgoun, Simon, and Salomi.

My time in Oxford has been profoundly marked by old and new friends who have shared the best and worst moments with me. My gratitude goes well beyond what I can express in these lines, but I am comforted by a long future of shared memories. Thank you to David, Leire, Alexia, Matt, Ollie, Marion, Simone, Ellie, Miren, Ane, Irene, Luxia, Laura, Sara, Myriam, Liam, Cynthia, Monty, Nacho, Juan, Sofía y Rodrigo. Admittedly, the story of the past few years would also be incomplete without everything I have learned from the Society of Spanish Researchers in the UK (SRUK/CERU) and, specifically, from Javi, Igor, and Carmen. Thank you.

My most heartfelt gratitude is for those who hold the deepest place in my memories. Amatxo, Papá, es gracias a vosotros que he aprendido a construir una casa propia. Bihotz bihotzez, eskerrik asko (zuen Menina). Lide, Felix, Nekane, Gemma, Honorio, Blanca, Ana, Rexu, mila esker zuen etxekotasun eta babesarengatik. Amona, Aitona, Alex, zuei ere bai.

Finalment, gràcies a tu. Has acompañado, impulsado, y transformado cada momento de estos últimos años y cada fracción de esta tesis.

"Escribo, ella escribió, que la memoria es frágil y el transcurso de una vida es muy breve y sucede todo tan de prisa, que no alcanzamos a ver la relación entre los acontecimientos, no podemos medir la consecuencia de los actos, creemos en la ficción del tiempo, en el presente, el pasado y el futuro, pero puede ser también que todo ocurra simultáneamente."

Isabel Allende, La Casa de los Espíritus

ABSTRACT

The world changes over time, but often in structured ways. In turn, temporal structures modulate cognitive processes ranging from perception to attention. This thesis investigates of how perception and attention are tuned to two kinds of temporal structures in the environment: feature regularities and temporal regularities. In **Chapter 2**, feature regularities across different timescales are found to jointly modulate perception. **Chapter 3** reveals that external attention is flexibly oriented to temporally regular visual and auditory features in the absence of spatial and motor certainty. Finally, **Chapter 4** unmasks that the prioritisation of sensory (visual and auditory) and action-related contents co-existing in working memory is flexible, temporally tuned, and yet functionally decoupled. Together, these findings unveil the ins and outs of how perception and attention are jointly guided by unique combinations of sensory contents and guidance signals such as expectations and task goals. Furthermore, the present thesis highlights the epistemological and methodological challenges posed by the temporal dimension and by cross-modality translation to the study of cognitive processes such as perception and attention. In summary, this thesis furthers our understanding of how regularities in sensory events unfolding in time, together with dynamic changes in the dispositions of our mental life, jointly modulate perception and attention.

STATEMENT OF CONTRIBUTIONS

The present thesis reflects the collaborative nature of research. Therefore, the presented studies are the result of the tireless work of people inside and outside of my supervisory team. The task design and analyses presented in **Chapter 2** of this thesis were developed in collaboration with Kia Nobre and Sage Boettcher. I collected the data and led the analyses and writing.

In **Chapter 3**, I worked together with Kia Nobre and Sage Boettcher to design the task and analysis procedures. I collaborated with Kerry Walker to translate the visual design to the auditory domain. I collected the data in Experiments 1 and 2. The data in Experiment 3 were collected with the help of Arden Tsang. I led the analyses and the writing. Part of the work presented in **Chapter 3** was published, and the final manuscript can be found here: https://doi.org/10.5334/joc.360. I have the co-authors' permission to include parts of the text in the present thesis.

The task design in **Chapter 4** also reflects the ideas of Freek van Ede, Sage Boettcher, and Kia Nobre. The translation from the visual to the auditory modality was done together with Kate Watkins. I led the data collection, with the help of Lola Milton-Jenkins (Experiment 1) and Pearl Young (Experiment 2). I performed the data analysis and writing. The writing of this thesis is my own and was carried out under the supervision of Kia Nobre.

CONTENTS

List of figures

LIST OF ABBREVIATIONS

EEG: electroencephalography

fMRI: functional magnetic resonance imaging

MEG: magnetoencephalography

TMS: transcranial magnetic stimulation

V1: primary visual cortex

PPC: posterior parietal cortex

FEF: frontal eye fields

ERP: event-related potential

LIP: lateral intraparietal area

IPS: intraparietal sulcus

PET: positron emission tomography

IPL: inferior parietal lobule

CNV: contingent negative variation

SRT: serial reaction-time task

MT: middle temporal visual area

NHP: non-human primate

CDA: contralateral delay activity

DVA: degree of visual angle

RT: reaction time

SD: standard deviation

ITI: inter-trial interval

ANOVA: analysis of variance

SEM: standard error of the mean

ISI: inter-stimulus interval

AUC: area under the curve

GLM: general linear model

GLMM: generalised linear mixed model

SMA: supplementary motor area

IT: inferior temporal cortex

MTL: medial temporal lobe

1 General introduction

1.1 General overview

Time is incessantly ticking. With it, the external world changes across all sensory modalities, the dispositions of our mental life (e.g., goals) wax and wane, and our bodies are in rapidly changing interaction with the environment (Nobre & van Ede, 2023). Cognitive processes ranging from perception to action, passing by attention and memory, are at the junction of these sources of flux and themselves unfold over time.

Given its layers of complexity, the temporal dimension poses substantial epistemological and technical challenges to the study of cognitive processes. Therefore, when studied in the laboratory, cognitive processes tend to be carefully extricated from their temporal embedding. However, studying cognitive processes as they ebb and flow is a key stride in the quest to comprehensively understand their inner workings.

The unfolding of the sensory environment over time is far from random. Instead, it is ubiquitously structured. For example, objects will land on the floor when dropped; thunder follows lightning; and cars move when the traffic light turns green. Cognitive processes are tuned to these environmental structures. The present thesis addresses some of the open questions about how perception and attention are tuned to different temporal structures in the environment.

In this thesis, the term "*temporal structures*" is used to encompass two kinds of predictable configurations of sensory events over time. First, sensory features that are recurrent in the environment (e.g., the downward motion of any falling object) and which are, therefore, repeatedly experienced over time will be referred to as feature regularities. Second, the temporal intervals between sensory events can be consistent, such as the cadence of someone's footsteps, which I will refer to as temporal regularities.

In the remainder of this introductory chapter, these two kinds of temporal structures will be presented. In the first section, regularities in stimulus features that unfold over different timescales will be introduced, and I will highlight their consequences on perception. This section contextualises **Chapter 2**. In the subsequent section, I will introduce different kinds of temporal regularities that are prevalent in our environments, and I will emphasize their effects as drivers of attention.

Next, I will define attention and differentiate between external and internal attention, which are at the centre of **Chapters 3** and **4**. First, I will turn to external attention and our current understanding of its neural underpinnings and behavioural consequences. I will specifically discuss the mechanisms whereby temporal regularities in the environment are thought to orient attention to moments in time. Additionally, some of the open questions about the inner workings of temporal attention will be highlighted, thus motivating the empirical work presented in **Chapter 3**.

Subsequently, internal attention will be presented and contrasted with its external counterpart, highlighting their similarities and differences. I will discuss some of the open questions about how internal attention is structured according to temporal regularities, which is at the core of **Chapter 4** of this thesis. Finally, I will briefly present some of the physiological markers of attention that will be harnessed in **Chapter 4**.

While most of the literature discussed in the next pages has focused on the visual system, the general principles are thought to generalise to other senses like audition. To explicitly test the generalisability of the present findings across sensory modalities,

Chapters 3 and **4** of this thesis pose their questions in both the visual and the auditory domains.

1.2 REGULARITIES

The external world is dynamic and ever-changing. It is also replete with structure across several attributes (e.g., Dong & Atick, 1995). For example, light tends to shine from above; orientations along the vertical and horizontal meridians are prevalent in forests and cities alike; and the footsteps of a family member walking along the house are consistent to the point of complete recognisability. A lifetime of exposure to these regularities has profound phenomenological, perceptual, and neural consequences. For example, the spatial distribution of light sources results in several perceptual illusions (Sun & Perona, 1998); cardinal biases towards the horizontal and vertical meridians can be measured in continuous orientation reports and are mirrored by long-lasting modulations in the tuning curves of V1 neurons (Gibson & Radner, 1937; Girshick et al., 2011); and neural oscillations can become entrained to rhythmic sensory stimuli (Lakatos et al., 2008).

Over time, regularities in our environments become predictable. They give rise to expectations about the *what*, *where*, and *when* of upcoming events. In turn, expectations[1] proactively prepare us for forthcoming occurrences, a process that is central to how we interact with a dynamically changing environment (Nobre & van Ede, 2023).

[1] In this thesis, I refer to the terms prediction and expectation devoid of their connotations in Bayesian probability theory, predictive coding, or related theoretical frameworks. Here, prediction refers to a regular structure that enables learning, and expectation indicates the state of the cognitive or neural system associated with the predicted event. Neither prediction nor expectation implies volition, awareness, or conscious deliberation.

1.2.1 Feature regularities across timescales and perceptual biases

As the footstep example above illustrates, regularities can unfold over multiple timescales and regularities across different timescales can co-occur and jointly guide perception[2]. Exposure to the same footstep pattern over years of cohabitation (long-term regularity) allows us to recognise the identity of the person walking through the house. In parallel, an increase in the loudness and pace of their footsteps (short-term regularity) foreshadows the moment when they will barge in through the door.

Exposure to repeated sensory features across different timescales has myriad consequences on perception and behaviour (for reviews see Clark, 2013; de Lange et al., 2018; Nobre & van Ede, 2018; Summerfield & de Lange, 2014). In addition to improving performance for the repeated features, it results in perceptual biases whereby any random feature is reported as systematically biased towards (more similar) or away (more dissimilar) from the regularly occurring feature (e.g., de Lange et al., 2018).

At the longest timescale, a lifetime of exposure to cardinal orientations results in perceptual biases towards such orientations (Girshick et al., 2011). Relatedly, exposure to an environment with stimuli from a particular feature distribution over hours results in central tendency biases whereby feature reports are biased towards the average feature (Hollingworth, 1910; Huttenlocher et al., 2000; Jazayeri & Shadlen, 2010).

Stimulus statistics can also be regular within the context of an ongoing task (medium-term regularities). For example, following exposure to repeated object configurations over tens of minutes, attention is directed towards the repeated configurations thus facilitating behaviour (Chun & Jiang, 1998; Zhao et al., 2013; for reviews see Chun, 2000; Fiser & Lengyel, 2022; Hutchinson & Turk-Browne, 2012; Schapiro & Turk-Browne, 2015). In addition to improving performance, medium-term

---

[2] See also Seriès & Seitz (2013) who distinguish between structural and contextual expectations.

regularities can also bias perception. For example, Scotti and colleagues (2021) reported that experiencing a frequent colour in an environment with a Gaussian colour distribution resulted in subtle perceptual biases to the regularly occurring colour in a subsequent attention task. Similarly, repeated exposure to two motion directions over an experimental session has been shown to bias orientation reports towards the repeated motion directions (Chalk et al., 2010; Gekas et al., 2013, 2015; see also Kok et al., 2013; Sotiropoulos et al., 2011).

Feature regularities over longer- and medium-term timescales are thought to be learned incidentally over time and to modulate perception implicitly (Fiser & Lengyel, 2022; Hutchinson & Turk-Browne, 2012; Schapiro & Turk-Browne, 2015). Furthermore, short-term feature regularities can also impact behaviour (i.e., predictive relations between neighbouring events). In the laboratory, short-term regularities are often cued or instructed and, therefore, deliberately used by participants (e.g., Posner, 1980; see **Section 1.4**). Predictive relations between adjacent events improve task performance and modulate underlying neural dynamics. For example, presenting participants with predictive cues about upcoming stimuli facilitates responses to the predicted stimulus (Posner, 1980). Expecting visual and auditory stimuli reduces neural activity in related sensory cortices (Summerfield et al., 2008; Todorovic et al., 2011). Despite a reduction in overall activity, fMRI and MEG studies have revealed the presence of underlying activity patterns specific to the expected feature, up to ~40 ms before its appearance (Aitken et al., 2020; Demarchi et al., 2019; Kok et al., 2012, 2013, 2017; see also Chelazzi et al., 1993; Luck et al., 1997; Martinez-Trujillo & Treue, 2004; Serences et al., 2009; Stokes et al., 2009).

Interestingly, perceptual biases have also been repeatedly reported between adjacent events that are unpredictive of each other. Namely, feature reports in trial N are systematically biased towards or away from the stimulus feature in the preceding trial (N-1). This phenomenon has been referred to as serial dependence, inter-trial bias, serial bias, or retrospective bias (Cicchini et al., 2014, 2024; Fischer & Whitney, 2014; Manassi et al., 2023; Pascucci et al., 2023; Thompson & Burr, 2009). Serial biases have been reported across different stimulus features, including orientations (Fischer &

Whitney, 2014), numerosity (Cicchini et al., 2014), facial attributes (Liberman et al., 2014; Taubert et al., 2016), body size (Alexi et al., 2018), motion (Czoschke et al., 2019), position (Papadimitriou et al., 2015), colour (Bays et al., 2009), ensemble properties (Manassi et al., 2017), etc.; in different sensory modalities (Motala et al., 2020); and in tasks with distinct purposes (for reviews see Cicchini et al., 2024; Manassi et al., 2023; Pascucci et al., 2023). Serial biases have also been reported in NHPs (Papadimitriou et al., 2015) and rodents (Akrami et al., 2018).

Given their ubiquitous nature, serial biases have been proposed to play a functional role in perception. Repulsive biases may increase sensitivity to small changes in the external world (Clifford, 2002; Clifford et al., 2007; Kohn, 2007; Thompson & Burr, 2009; Weber et al., 2019; Webster, 2015) and attractive biases may promote the continuity and stability of visual perception in a smoothly varying environment (Cicchini et al., 2018; Czoschke et al., 2019; Fischer et al., 2020; Fischer & Whitney, 2014; Manassi & Whitney, 2022). Broadly, serial biases have been suggested to reflect an adaptation to the global statistics of the visual environment (Barbosa & Compte, 2020; Cicchini et al., 2018; Clifford et al., 2007; Felsen et al., 2005; Fischer & Whitney, 2014; Kiyonaga et al., 2017; Panichello et al., 2019; van Bergen & Jehee, 2019; Weber et al., 2019).

Nevertheless, as noted in recent reports (Blondé et al., 2023; Kalm & Norris, 2018; Tong & Dubé, 2022), studies investigating serial dependence have mostly deployed stimuli with uniform (random) feature distributions. By construction, therefore, no statistical regularities were present in most of these tasks. Consequently, several open questions remain regarding the effects of statistical regularities on serial biases.

Recent studies about the consequences of feature distribution manipulations on serial biases have started to shed light on their interrelations. For example, exposure to facial attributes considered stable (gender) vs changeable (facial expression) resulted in serial biases in opposite directions. The attractive serial bias observed for gender was thought to promote stability in visual perception when the visual context was constant. Alternatively, the repulsive serial bias reported for facial expressions was suggested to reflect increased sensitivity to changes in a volatile environment (Taubert et al., 2016). Blondé and colleagues (2023) also noted differences in the direction of serial biases as a function of whether gratings were sampled from a uniform or Gaussian distribution (see also Chopin & Mamassian, 2012; Gekas et al., 2019; Panichello et al., 2019). On the whole, serial biases seem to be influenced by exposure to feature regularities.

Additionally, recent studies have described interactions between serial biases and biases arising from exposure to longer-term feature regularities such as the central tendency effect (Bae, 2024; but see Cicchini et al., 2022; Galluzzi et al., 2022; Lieder et al., 2019; Saarela et al., 2023). Consistently, computational models better describe the behavioural effects of serial dependence when they include parameters capturing both the immediate past and longer-term statistics (Chopin & Mamassian, 2012; Gekas et al., 2019; Glasauer & Shi, 2022; Kalm & Norris, 2018; Papadimitriou et al., 2015; Tong & Dubé, 2022; van Bergen & Jehee, 2019). Interestingly, a recent study revealed that optogenetically inactivating the PPC in rodents resulted in the simultaneous ablation of two perceptual biases: the contraction bias towards the average feature of several past observations (medium-term regularity) and the serial bias to the immediately preceding event (Akrami et al., 2018). This and other studies (Boboeva et al., 2023; Papadimitriou et al., 2015) point to potential commonalities underlying perceptual biases that emerge from extended exposure to statistically structured environments and temporal adjacency between random visual features.

Moreover, Hahn and Wei (2024) recently presented a Bayesian framework that jointly accounts for the perceptual biases elicited by immediately preceding events and longer-term exposure to feature regularities (see also Chopin & Mamassian, 2012; Gekas et al., 2019; Kalm & Norris, 2018; Tong & Dubé, 2022; van Bergen & Jehee, 2019). In their model, feature regularities and temporal adjacency between events modulated different processing stages – priors and encoding modules, respectively. Interestingly, the same Bayesian framework also simultaneously accounts for the two directions across which perceptual biases emerge (repulsive and attractive), an oddity whose significance remains debated in the field (Fritsche et al., 2020; Gekas et al., 2019; Moon & Kwon, 2022; Pascucci et al., 2019).

In summary, perceptual biases to regular features emerge following exposure to statistically structured environments across different timescales. In parallel, visual stimuli bias the perception of immediately upcoming (unpredictable) events. While they have been investigated mostly separately, recent studies suggest that these two kinds of perceptual biases co-occur, interact, and may even reflect the same underlying process. Nevertheless, several open questions remain about whether and how perception is jointly biased by temporal adjacency between random visual events and by regularities over shorter (predictive relations between neighbouring events) and longer (prolonged exposure to statistical structures) timescales. In **Chapter 2** of the present thesis, I aim to address some of these open questions.

1.2.2 Temporal regularities

In addition to regularities in stimulus features, regularities in the temporal intervals between events (temporal regularities) are also ubiquitous in the environment. For example, rhythms are found in everyday sounds such as footsteps, speech, or music. Over time, consistent temporal relations become predictable and lead to the formation of expectations about the timing of forthcoming events. In turn, temporal expectations proactively guide cognitive processes such as perception and attention (Nobre & van Ede, 2018). The usage of temporal information in the service of other cognitive processes is referred to as implicit timing, which contrasts with tasks in which time itself is the reported feature (explicit timing; Coull & Nobre, 2008). In this thesis, I am specifically concerned with how temporal regularities guide attention, a form of implicit timing (see **Section 1.4.2**).

Like feature regularities, temporal regularities can be learned incidentally from experience. A prominent example is exposure to predictable distributions of event occurrence probability (hazard function; Luce, 1991). For example, the probability of the bus coming given that it has not yet arrived increases with time spent at the bus stop. Alternatively, the probability of hearing an answer increases steeply following the formulation of a question but decreases thereafter. The consequences of predicably changing temporal probabilities on behaviour have mostly been studied using tasks in which a warning stimulus signals the appearance of another stimulus following an interval (foreperiod; Los, 2010; Niemi & Naatanen, 1981; Woodrow, 1914). In these tasks, the probability distribution of foreperiod duration is manipulated and participants are exposed to one or several hazard functions. Following exposure to a given hazard function, temporal expectations are formed which, in turn, facilitate task performance (Los, 2010; Thomaschke & Dreisbach, 2013; Trillenberg et al., 2000; van Elswijk et al., 2007; Vangkilde et al., 2012, 2013; see also **Section 1.4.2.2**).

Moreover, exposure to consistent temporal configurations over tens of minutes guides the subsequent orienting of attention to the relevant points in time (temporal contextual cueing; Olson & Chun, 2001; see also Cravo et al., 2017; Zhao et al., 2013). Temporal expectations can also be reliably elicited by isochronous rhythms (Jones, 1976; Large & Jones, 1999; Morillon et al., 2015; Sanabria et al., 2011) and by more complex sequences of events with recurrent temporal structuring (Heideman, et al., 2018a, 2018b, 2018c; Kornysheva et al., 2013; O'Reilly et al., 2008; Shin & Ivry, 2002), both of which have facilitatory effects on behaviour.

In addition to the incidental learning of temporal regularities over time, specific event timings can be voluntarily prioritised. For example, the consistent timing between pressing down on the toaster and hearing it pop can be used to retrieve the toast at the right time, while making coffee in the meantime. The process of orienting attention based on temporal expectations and task relevance (Coull & Nobre, 1998; Griffin et al., 2002) is key for the present thesis, and will be further discussed below.

1.3 ATTENTION

Selective attention (hereafter 'attention') is the process of anticipating, prioritising, selecting, routing, integrating, and preparing[3] relevant contents to guide adaptive behaviour (Nobre, 2018; Nobre & Kastner, 2014; Nobre & van Ede, 2023). Attention can be driven by a variety of signals, including goals, motivations, physical salience, and/or expectations. The latter can emerge following exposure to regularities across multiple timescales, such as those introduced in **Section 1.2.1**.

Attention can be described along several axes, including covert vs overt attention, depending on whether the eyes move to the attended attribute; and endogenous vs exogenous attention, according to whether it is voluntarily directed or involuntarily captured (for reviews see Carrasco, 2011; Nobre, 2018; Nobre & Kastner, 2014). An additional dimension of attention is given by the nature of its targets. Attention can be directed towards events in the sensory stream (external attention) or towards internal, mnemonic contents (internal attention; Chun et al., 2011; Gazzaley & Nobre, 2012; Nobre & van Ede, 2023; Souza & Oberauer, 2016; Stokes & Nobre, 2012). Each of these processes is presented in **Sections 1.4** and **1.5**, respectively.

Finally, attention is dynamic, and it is tuned to temporal regularities like the ones introduced in **Section 1.2.2** (Nobre & Rohenkohl, 2014; Nobre & van Ede, 2018, 2023). The present thesis focuses on the covert, endogenous orienting of both external and internal attention. I am particularly interested in how attention is structured along the temporal dimension.

1.4 External attention

External attention is the process of prioritising external information to guide behaviour. In the laboratory, the focus of attention has often been manipulated using

---

[3] The term "prioritise" is hereafter used to signify the broader range of functions that constitute selective attention: anticipating, prioritising, selecting, routing, integrating, and preparing.

instructions or cues. In early manipulations, participants were instructed to attend to one out of multiple streams of concurrent stimulation. Multiple-stream tasks highlighted the ability of attention to selectively focus on specific contents and *filter out* others. For example, participants were instructed to attend to one of two auditory streams being played from the left and the right side, respectively (Cherry, 1953). The contents of the attended stream were consistently remembered more accurately and salient changes in the unattended stream often went unnoticed.

Over the years, multiple-stream tasks were refined, and researchers began to compare the speed and accuracy of target detection in attended and unattended streams. Attending one stream was found to result in improved performance and increased neural responsiveness to the attended contents. This came together with behavioural costs and an absence of neural response modulations to the unattended stream (Choi et al., 2014; Hillyard et al., 1973; Lange & Röder, 2010, 2010; Spence & Driver, 1994; Woldorff et al., 1993). In addition to locations, listeners can also direct their attention to other auditory features such as talker identity, pitch, or timbre (Mondor & Amirault, 1998; Shinn-Cunningham & Best, 2008). Moreover, multiple-stream tasks have also been used to investigate the orienting of attention to various visual features (Hillyard & Anllo-Vento, 1998; Luck et al., 1990; Mangun et al., 1993).

In 1980, Posner developed a task in which the focus of attention was manipulated flexibly using cues that changed on a trial-by-trial basis (Posner, 1980). This flexible orienting of attention based on changing goals reflects a key aspect of how attention is used in daily tasks. In a standard trial of this symbolic cueing task, participants are centrally presented with a symbolic cue indicating one out of a set of possible locations. Following a brief delay, a target is shown, and participants respond accordingly.

In symbolic cueing tasks, cues can be predictive or instructive. Predictive cues signal the probability of event occurrence. In predictable spatial cueing, the cue indicates the most likely location for the target to appear (e.g., 80%). In turn, attention is oriented to the cued location for detecting or discriminating the target (Posner, 1980). Alternatively, instructive cues signal which out of several equally likely stimuli is relevant in a given trial. Thus, attention can also be oriented based on goals (Kastner et al., 1999; Luck et al., 1997; Moran & Desimone, 1985; Serences et al., 2004). Attention orienting can therefore be driven by expectations or goals. In several cases, it is driven concurrently by both. Interestingly, attention based on expectations vs goals seems to have separable behavioural consequences (Bang & Rahnev, 2017; Jiang et al., 2013; Rungratsameetaweemana et al., 2018; Wyart et al., 2012), suggesting distinct modulatory neural mechanisms (Rungratsameetaweemana & Serences, 2019; Summerfield & de Lange, 2014).

Importantly, cueing participants (with instructive and predictive cues) to target locations confers ample benefits on performance in comparison to neutral and invalid cues (Carrasco et al., 2000; Hawkins et al., 1990; Posner, 1980; Yeshurun & Carrasco, 1998). Several subsequent studies using similar designs have confirmed that attention can also be oriented to objects (O'Craven et al., 1999; Scholl, 2001), features (Liu et al., 2007; Maunsell & Treue, 2006; Treue & Martínez Trujillo, 1999), semantic categories (Cristescu et al., 2006; Cristescu & Nobre, 2008; Posner & Snyder, 2004), motor actions (Rushworth et al., 2001, 2003) and several others. Additionally, selectively attending a location leads to both behavioural advantages to detect events at attended locations and behavioural costs for events at unattended locations (Pestilli & Carrasco, 2005). This highlights how attention arbitrates between competing contents, directing neural and cognitive resources to selectively process relevant over irrelevant attributes (Carrasco, 2011; Nobre, 2018).

In the everyday world, however, attention is rarely driven by explicit symbolic cues. Returning to one of the earlier examples, when looking for the source of light in a visual scene, attention is not directed upwards by the appearance of an arrow in the centre of the visual field. Instead, it is oriented towards the top of the scene based on past experiences about the likely source of light (predictions/expectations).

This incidental learning of regularities in the environment which, in turn, orients attention to the relevant sensory attributes has been studied using contextual cueing tasks (Chun & Jiang, 1998). In these tasks, participants are shown repeated configurations of objects over blocks. Following prolonged exposure, participants' responses to the regular configurations are enhanced compared to responses to new object configurations (Chun, 2000; Chun & Jiang, 1998; Zhao et al., 2013).

On the one hand, contextual cueing emphasises the incidental pick-up of environmental regularities and their subsequent usage to orient attention (i.e., looking upwards when searching for a light source). On the other hand, trial-wise manipulations of instructive cues emphasise the flexible allocation of attention based on changing task goals. For example, attention may be directed upwards because of an attempt to gauge the weather or to follow a bird's path (goals). Both are key features of how attention operates during natural behaviour, and they often act in unison. Therefore, to investigate how attention is concurrently shaped by the incidental pick-up of temporal regularities and driven by flexibly changing goals, the task presented in **Chapter 3** of this thesis encompasses features of both processes.

1.4.1 Attention to space and sensory features

The first clues about the neural underpinnings of (visual) attention came from patients with hemispatial neglect. In the absence of general sensory or motor deficits, they were unable to attend to stimuli on the visual field contralateral to their lesion (Driver & Vuilleumier, 2001; Heilman & Van Den Abell, 1980; Kinsbourne, 1970; Mesulam, 1981). Neglect is recognised as a complex syndrome resulting from damage to a large-scale network of brain regions regulating spatial attention and cognition (Mesulam, 1999). The lesions that most commonly result in hemispatial neglect encompass parietal areas (Mort et al., 2003; Nobre & Kastner, 2014), but neglect can also occur after frontal, temporal, thalamic, or striatal lesions (Husain & Rorden, 2003; Karnath et al., 2002).

Complementing the neuropsychology literature, single-unit studies in NHPs revealed that the goal-directed orienting of attention modulated firing rates of neurons across the parietal cortex (Mountcastle et al., 1975), FEF (Goldberg & Bushnell, 1981), and superior colliculus (Wurtz & Goldberg, 1972), among others. Together, these observations vindicated the proposal that large-scale brain networks composed of key frontoparietal cortical nodes[4], through their inter-connections with other cortical (sensory, motor, and associative) and subcortical areas, orchestrated attentional control (Mesulam, 1981, 1990, 1999; Nobre & Kastner, 2014; Nobre & Mesulam, 2014).

Subsequently, human neuroimaging experiments using predictive cueing tasks to manipulate spatial, object-, and feature-based attention confirmed the consistent involvement of dorsal frontal and parietal cortical areas in attentional control (Corbetta et al., 1993, 1995; Nobre et al., 1997; Serences & Boynton, 2007). These studies also highlighted the anatomical overlap between spatial attention and oculomotor control, even in the absence of eye movements (Corbetta et al., 1998; Nobre et al., 1997, 2000). This and related findings led to the proposal of the frontoparietal network as responsible for controlling spatial attention through the integration of multimodal sensory stimuli, action intentions, and motivational states (Mesulam, 1990; Nobre & Mesulam, 2014).

The dorsal frontoparietal network is thought to act by feeding back into sensory areas and modulating their activity (Kastner & Ungerleider, 2001; Nobre & Kastner, 2014). Stimulation of a key node of this network, the FEF, has attention-like effects, as reflected both behaviourally and in its downstream modulations of V4 activity in NHPs (Moore & Fallah, 2004). Similarly, TMS-induced pulses over FEF modulates visual processing as measured with fMRI and ERPs in a manner that is reminiscent of attention (Ruff et al., 2006; Taylor et al., 2007).

These top-down modulatory signals are thought to act selectively on feature-sensitive neurons and their receptive fields (Kastner & Ungerleider, 2001). Neural responses to attended sensory attributes (locations and other features) are enhanced in single-neuron recordings across visual areas in NHPs (Cohen & Maunsell, 2011; Luck

[4] While the specific areas included in this frontoparietal network vary across descriptions, several regions seem to be consistently involved: frontal areas, including the FEF, and posterior parietal areas, such as the LIP (Boshra & Kastner, 2022; Nobre, 2018).

et al., 1997; Martinez-Trujillo & Treue, 2004; Moran & Desimone, 1985; Reynolds et al., 1999; Treue & Martínez Trujillo, 1999; Womelsdorf et al., 2006). Comparable modulations have also been reported with neuroimaging in humans (Corbetta et al., 1993; Gandhi et al., 1999; Hopf et al., 2004; Kastner et al., 1999; Mangun et al., 1997; Serences et al., 2004; Serences & Boynton, 2007). In addition to enhancing the responses of feature-sensitive neurons, selective attention can increase their baseline activity, their response sensitivity, and their cross-coupling, as well as filter out irrelevant information (Carrasco, 2011; Fries et al., 2001, 2008; Kastner & Ungerleider, 2001).

Accordingly, most theoretical models of attention place neuronal receptive fields at their centre (Nobre & Kastner, 2014; Reynolds & Chelazzi, 2004; Reynolds & Heeger, 2009). For example, according to the Biased Competition Model, attention acts by biasing neural processing towards prioritised visual attributes and at the expense of processing unattended attributes (Desimone & Duncan, 1995). More specifically, stimuli within a neuron's receptive field would compete for its processing resources. Attention acts by biasing competition in favour of the attended stimulus, which, in turn, facilitates the integration of the various features defining the target stimulus.

Attention modulates multiple stages of processing. Neuronal modulation has been reported across different sensory and higher-level areas (Kastner & Ungerleider, 2001; Nobre, 2018; Nobre & Kastner, 2014). EEG studies have noted modulations from early sensory ERPs, such as P1 and N1 in the case of visual spatial attention, to later stages of visual selection processes (N2PC) and decision- and response-related potentials (e.g., P300; Eimer, 1998; Mangun, 1995).

The modulation of sensory activity can also be anticipatory, preceding the appearance of the cued stimulus. Anticipatory changes include modulations in baseline firing rates that may interact with sensory processing to bias competitive interactions (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001). Consistently, both NHP single-unit recordings (Chelazzi et al., 1993, 1998; Luck et al., 1997) and fMRI studies in humans (Kastner et al., 1999; Reddy et al., 2009; Stokes et al., 2009) have revealed anticipatory modulations in content-specific activity. Additionally, the proactive allocation of attention has been linked with general and location-specific attenuations of alpha-frequency activity (8-12 Hz; Foxe et al., 1998; Thut et al., 2006; Worden et al., 2000; see **Section 1.6.1**).

A similar set of principles is thought to underlie attention in other sensory modalities. Auditory attention engages a frontoparietal network that is reminiscent but distinct from the network consistently reported in visual attention (Lee et al., 2014; Spence & Santangelo, 2010; Zatorre et al., 1999). Interestingly, some of the frontal regions activated by auditory attention seem to be anatomically interleaved with frontal areas consistently reported in visual attention (Braga et al., 2013; Michalka et al., 2015, 2016; Noyce et al., 2017). Early processing in the auditory cortex is modulated by attention in a content-specific fashion (e.g., Petkov et al., 2004; Woldorff et al., 1993; Woodruff et al., 1996; Woods et al., 1992). The modulatory effects of auditory attention have also been observed in early stages of auditory processing in subcortical areas (Forte et al., 2017; Galbraith & Arroyo, 1993).

In summary, external attention engages a frontoparietal network, which is bidirectionally connected to other higher-level areas, sensory and motor cortices, and subcortical structures. This frontoparietal network is thought to modulate downstream sensory activity by harnessing neuronal receptive fields. However, attention can be directed to attributes without dedicated receptive fields such as semantic contents (Cristescu et al., 2006; Cristescu & Nobre, 2008; Posner & Snyder, 2004) and, most importantly for this thesis, moments in time.

1.4.2 Orienting attention to moments in time

Attention unfolds in changing environments. It must therefore operate flexibly and dynamically. Fittingly, in addition to being directed towards locations and other sensory attributes, attention can also be directed to specific moments in time (Coull &

Nobre, 1998; see also Kingstone, 1992). Building on Posner's cueing task (Posner, 1980), Coull and Nobre (1998) presented participants with predictive cues about the location, timing, or joint location and timing of a subsequent target. Participants were consistently faster at detecting targets appearing not only at the predicted locations but also at the predicted times regardless of their location, and at the expected spatiotemporal combinations (see also Coull et al., 2000; Griffin et al., 2001; Kingstone, 1992; Miniussi et al., 1999; Nobre, 2001).

Behaviourally, benefits occur for identifying stimuli at attended moments and costs occur for stimuli at unattended moments (Coull & Nobre, 1998). Temporal attention results in perceptual trade-offs between attended and unattended moments (Denison et al., 2017, 2021; Fernández et al., 2019). Therefore, analogous to spatial attention, temporal attention is directed selectively to relevant points in time, at a cost for other times.

The allocation of attention to points in time shares undeniable similarities with how it is oriented to locations and other sensory features. Nevertheless, there are no temporal receptive fields that are comparable to those for space and other features (Coull et al., 2011; Muller & Nobre, 2014; but see Eichenbaum, 2014; Theunissen et al., 2000). Therefore, several open questions remain about which processing stages are modulated by temporal attention and how.

1.4.2.1 Sources and purposes of temporal attention

Temporal expectations can arise from different types of temporal regularities. They can have different consequences on attention and may rely on separable neural systems (Bouwer et al., 2020; Breska & Deouell, 2014; Breska & Ivry, 2018; de la Rosa et al., 2012; Rohenkohl et al., 2011; Tal-Perry & Yuval-Greenberg, 2022; Triviño et al., 2011). For example, in contrast to the benefits conferred by symbolic temporal cues, the behavioural benefits of rhythms seem to be independent of task instructions, competing task demands, and predictive value (Breska & Deouell, 2014; Capizzi et al., 2012, 2013; de la Rosa et al., 2012; Rohenkohl et al., 2011; Sanabria et al., 2011). Based on this, rhythms have been proposed to engage exogenous temporal attention (Coull & Nobre, 2008; Jones et al., 2002; Rohenkohl et al., 2011). In contrast, endogenous temporal attention can be oriented flexibly and voluntarily to the anticipated timing of task-relevant events (Coull & Nobre, 1998).

Another important determinant of the consequences of temporal attention is the purpose of a given task (Shalev et al., 2019). van Ede and colleagues (2020) investigated the behavioural and neural consequences of spatiotemporal expectations following predictive cues in two tasks using MEG. One required speeded responses to salient stimuli, while the other required fine sensory discrimination. Interestingly, when the purpose of the task was to respond rapidly, temporal expectations sped participants' responses and modulated beta-frequency (13-30 Hz) activity over motor cortices, a known marker of motor preparation (e.g., Kaiser et al., 2001; see **Section 1.6.2**). Alternatively, when visual discrimination was the primary goal of the task, improving accuracy was the main behavioural consequence and alpha-frequency (8-12 Hz) activity over occipital (visual) areas showed the strongest modulation (e.g., Foxe et al., 1998; see **Section 1.6.1**). In a brain-imaging task, a key brain area implicated in controlling temporal attention, the left IPS, was found to be involved in temporal orienting irrespective of whether the purpose of the task was perceptual or motor. However, its connectivity with sensory and motor cortical areas depended on the perceptual or motor nature of the task (Davranche et al., 2011).

Consistent with the variety of sources and purposes that differentially drive temporal attention, its consequences on behaviour are also varied. In addition to speeding responses, temporal attention can modulate response accuracy (Correa et al., 2005; Davranche et al., 2011; Rohenkohl et al., 2014; Samaha et al., 2015), improve perceptual discriminability and contrast sensitivity (Correa et al., 2005; Cravo et al., 2013; Fernández et al., 2019; Rohenkohl et al., 2012; Rolke & Hofmann, 2007), modulate decision and non-decision processes (Jepma et al., 2012; van den Brink et al., 2021), and facilitate multisensory coupling (Bauer et al., 2021). Moreover, cueing temporal intervals can partially overcome the detrimental effects of the so-called attentional blink (Martens & Johnson, 2005), suggesting that temporal attention can increase visual temporal resolution. Moreover, temporally expected irrelevant features (distractors) in visual search tasks are suppressed more efficiently (Amit et al., 2019; Los, 2004; Seibold & Rolke, 2014; Xu et al., 2021, 2022; but see Balke et al., 2021).

1.4.2.2 Time and actions

Since the early studies about the flexible orienting of temporal attention, the latter was noted to be tightly linked with motor functions (Coull & Nobre, 1998). PET and fMRI activity patterns revealed that spatial and temporal attention engaged some overlapping regions in the dorsal frontoparietal network (Coull et al., 2000, 2001; Coull & Nobre, 1998). However, temporal orienting additionally selectively engaged the left IPS, the left premotor cortex and the left anterior IPL (Coull & Nobre, 1998). Importantly, the left IPS has also been implicated in selecting and preparing delayed manual actions (motor orienting; Rushworth et al., 2003), which require fine temporal control.

Several subsequent studies have replicated a left-lateralised network of regions for temporal orienting, including areas related to action preparation such as the left IPS, the left premotor cortex, and the bilateral cerebellum (Cotti et al., 2011; Coull et al., 2000, 2011; Coull & Nobre, 1998; Davranche et al., 2011; Ivry et al., 2002; Nobre & Rohenkohl, 2014; O'Reilly et al., 2008). Additionally, temporal attention has been repeatedly shown to modulate ERP markers of anticipation and motor preparation such as the CNV (Capizzi et al., 2013; Correa et al., 2006; Griffin et al., 2002; Macar & Vidal, 2004; Mento, 2013; Miniussi et al., 1999; Pfeuty et al., 2005).

Given the consistent overlap between the brain areas and processes engaged in temporal orienting and manual action preparation, temporal attention has been proposed to have a close relation to the functional architecture of manual-control circuits (Nobre, 2001; O'Reilly et al., 2008). Similar to how spatial attention is thought to build on the spatial acuity and computations of the oculomotor control system (e.g., Sheliga et al., 1994), temporal orienting has been proposed to harness the temporal granularity of hand movements.

Consistently, temporal attention has strong modulatory effects on motor processing. For example, cued temporal attention consistently enhances the amplitude and shortens the latency of late decision- and response-related P300-like potentials (Correa et al., 2006; Correa & Nobre, 2008; Doherty et al., 2005; Griffin et al., 2001, 2002; Miniussi et al., 1999). Hazard-function and foreperiod manipulations influence single-neuron activity patterns over motor areas such as the primary motor cortex (Riehle et al., 1997), premotor areas (Lucchetti & Bon, 2001), the SMA (Heinen & Liu, 1997), and the LIP (Janssen & Shadlen, 2005; Kilavik & Riehle, 2010). Additionally, isochronous rhythms are thought to modulate sensory processing by entraining motor circuits (Morillon et al., 2015; Morillon & Baillet, 2017). Complex temporal sequences, as studied using SRT tasks, have been shown to modulate action-related beta-frequency (13-30 Hz) activity in a temporally tuned fashion (Heideman et al., 2018b).

One outstanding question about the effects of temporal attention on motor processes is whether it exerts a widespread modulatory influence or whether it acts by targeting specific motor programmes. Relatedly, a longstanding debate grapples with the question of whether the timing of sequential movements is encoded independently from their corresponding effectors or, alternatively, whether the representation of sequence timing is necessarily coupled with specific movements[5] (Conditt & Mussa-Ivaldi, 1999; Shin & Ivry, 2002; Spencer & Ivry, 2009). Some studies have reported that, over time, the representation of sequence timings in an SRT task becomes decoupled from the effectors until timing is represented independently (Kornysheva, 2016; Kornysheva et al., 2013; Kornysheva & Diedrichsen, 2014). Alternatively, others have suggested that the temporal structure of a sequence of movements is bound to

---

[5] This is part of a longstanding debate about whether time is represented in dedicated neural systems (e.g., Gibbon et al., 1984; Treisman, 1963) or whether temporal information is embedded in all neural circuits (e.g., Mauk & Buonomano, 2004). For reviews see Coull et al., (2011) and Muller & Nobre (2014).

the corresponding effectors and actions (Nobre et al., 2007; O'Reilly et al., 2008; Shin & Ivry, 2002).

Cotti and colleagues (2011) used symbolic cues to orient participants' attention either to moments in time, to specific motor effectors (hand and eye), or to a combination of both. Importantly, they found that temporal orienting could benefit behaviour even when the effector was uncertain. Building on these studies, one of the motivations for **Chapter 2** of this thesis is to investigate whether (visual and auditory) temporal expectations formed from incidentally learned temporal regularities facilitate behaviour in the absence of certainty about motor effectors.

Importantly, while temporal orienting has strong modulatory effects on motor processes, it has also been found to influence the processing of sensory attributes, particularly space.

1.4.2.3 Time and space

The interdependence between time and space is part of a longstanding debate in both physics and neuroscience (Buonomano & Rovelli, 2021). Some accounts have suggested that timing is intrinsically and irrevocably bound to spatial processing (Buonomano & Maass, 2009; Cai et al., 2012; for review see Muller & Nobre, 2014). However, other proposals emphasise their independent representation and modulation of cognitive processes (e.g., Ivry & Schlerf, 2008; Treisman, 1963).

Spatiotemporal expectations have been consistently shown to direct attention efficiently to the predicted spatiotemporal combinations both in vision and audition (Boettcher et al., 2022; Lange & Röder, 2010; Pfeuffer et al., 2020; Rieth & Huber, 2013; Thomaschke et al., 2016; Thomaschke & Dreisbach, 2013; Wagener & Hoffmann, 2010). However, most studies have not directly tested whether spatial and temporal attention act independently or in synergy.

Studies which have addressed this question have reported mixed effects. For example, Coull & Nobre (1998) found additive effects of temporal and spatial orienting (see also Coull et al., 2001; Griffin et al., 2002; Miniussi et al., 1999). In contrast, other studies have noted strong interactions between spatial and temporal attention. Doherty and colleagues (2005) studied incidentally formed temporal, spatial, and spatiotemporal expectations, which directed participants' attention to relevant moments and/or locations. In this task, a ball moved in discrete steps across a display and disappeared underneath an occluding bar. As a manipulation of temporal expectations, the interval between successive steps was either regular (rhythmic) or irregular. Independently, the location of ball reappearance could be spatially predictable or unpredictable. Both temporal and spatial predictions enhanced performance, but their behavioural effects did not interact (Doherty et al., 2005; see also Correa & Nobre, 2008; Kingstone, 1992; Praamstra et al., 2006; Rohenkohl & Nobre, 2011). Strikingly, despite the additive nature of the behavioural effects, a strong interaction was observed in the modulations of early visual processing stages (P1). While temporal expectations alone did not modulate P1, spatiotemporal expectations significantly enhanced P1 magnitude relative to spatial expectations alone. The lack of a behavioural interaction observed in Doherty and colleagues' study (2005) was speculated to result from the relatively low perceptual demands of the task. Consistently, a perceptually demanding symbolic cueing task revealed a strong interaction between spatial and temporal attention at the behavioural level. Specifically, the benefits of temporal expectations for discrimination were limited to spatially attended locations (Nobre & Rohenkohl, 2014; see also Milliken et al., 2003; Seibold et al., 2020). Similarly, in a temporally structured SRT task, isolated temporal sequences were ineffective in facilitating behaviour, but combined spatiotemporal expectations led to a striking amplification of the behavioural effects of isolated spatial expectations (O'Reilly et al., 2008).

In the auditory domain, Lange and colleagues (2006) manipulated temporal attention in blocks (long vs short foreperiod) and independently from spatial attention. While both spatial and temporal attention facilitated performance, temporal attention only did so at unattended locations and spatial attention improved behaviour at unattended times exclusively. Therefore, while an interaction between temporal and spatial auditory attention was identified, it followed a very different pattern to visual temporal attention (Lange et al., 2006). In addition to different modalities, the above-presented studies manipulated different kinds of temporal regularities to orient attention (e.g., blocked foreperiods, rhythms, and symbolic temporal cueing) which could partially account for the observed differences (see **Section 1.4.2.1**).

Interestingly, cellular recordings in macaques also support a strong link between temporal and spatial attention. For example, the effects of spatial attention on V4 activity varied in amplitude according to the blocked manipulations of temporal hazard functions for target appearance (Ghose & Maunsell, 2002). Ghose and Bearl (2010) further found that spatial receptive fields of MT neurons changed across brief time ranges as a function of spatiotemporal expectations.

Together, these findings inspired the proposal that the temporal orienting of attention may act by latching onto other stimulus attributes. In particular, temporal attention may modulate activity in neurons with spatial receptive fields in a temporally tuned fashion (Nobre, 2010; Nobre & Rohenkohl, 2014). This idea additionally motivated the studies presented in **Chapter 3** of this thesis.

1.4.2.4 Time and sensory features

Temporal attention can also be guided by non-spatial and non-motor attributes such as colours, images, orientations, or tones (Anderson & Sheinberg, 2008; Jaramillo & Zador, 2011; Kingstone, 1992; Lakatos et al., 2013; Seibold et al., 2020; Warren et al., 2014). However, most studies investigating feature-temporal attention have not manipulated spatial certainty or have not introduced strong spatial competition between attended items. Therefore, in these studies, the attended stimuli were spatially predictable and the modulations of temporal attention on non-spatial (and non-motor) processes could not be isolated.

For example, Anderson and Sheinberg (2008) developed a temporal-cueing task which manipulated temporal expectations on a trial-by-trial basis in NHPs. Temporally expected images increased the firing rates of image-selective neurons in IT and enhanced inter-spike coherence (see also Fries et al., 2001, 2008). Using fMRI, Warren and colleagues (2014) found that V1 orientation-tuning to attended orientations was amplified in an anticipatory fashion in a temporal cueing task. In the auditory domain, Jaramillo and Zador (2011) trained rats to discriminate between two target tones of different frequencies. Across two different kinds of blocks, target tones were more likely to happen following a short or a long foreperiod. Interestingly, temporal expectations enhanced the neural responses of frequency-tuned auditory cortex neurons in a temporally specific fashion. Nevertheless, in all these studies, the expected features were also spatially predictable.

To my knowledge, one study has provided preliminary evidence that temporal attention may modulate feature-specific neural activity independent of spatial receptive fields. Lima and colleagues (2011) explored the effects of temporal orienting in V1 neurons during flexible, trial-by-trial cueing of spatially predictable targets. Temporal expectations increased gamma-frequency activity (spiking, LFP, and coherence) that was temporally selective but anatomically widespread, encompassing neurons with disparate spatial receptive fields (Lima et al., 2011). Interestingly, this increase in gamma-frequency activity was accompanied by a reduction in alpha-frequency activity, consistent with the findings of studies using human non-invasive recordings (Rohenkohl & Nobre, 2011). This study therefore pointed to a temporally specific modulation of spatially widespread receptive fields in V1, even when targets were spatially predictable.

Only a handful of studies have investigated the behavioural consequences of temporal attention under spatial and motor uncertainty, and, to the best of my knowledge, none has tested the flexible orienting of temporal attention under spatial and motor uncertainty. Olson and Chun (2001) investigated contextual cueing of temporal attention by presenting participants with streams of letters, some of which were organised into temporal sequences. If a temporally structured sequence of elements preceded the appearance of a target, responses to the target were faster, despite a lack of spatial predictability. Similarly, Seibold and colleagues (2020) found that exposure to blocked foreperiods could improve performance to sensory features in the absence of spatial certainty. Interestingly, they also found that temporal attention interacted with both spatial and feature-based attention, supporting the proposal that temporal expectations act by latching onto other stimulus attributes. These studies suggest that incidentally learned temporal regularities can orient attention in the absence of spatial certainty.

Vangkilde and colleagues (2012; experiments 2 and 3) found that blocked exposure to two different hazard functions directed temporal attention to letters in the absence of spatial certainty. Interestingly, in this task, responses were not speeded, further revealing that temporal attention facilitated performance in the absence of full motor certainty. In a visual search task, Grubert and Eimer (2018) found that feature-specific attention (irrespective of location), as indexed by ERP modulations, was activated in a temporally tuned and anticipatory fashion. However, in these studies, the manipulation of temporal expectations was blocked and, therefore, did not tap into the flexible nature of temporal orienting. Additionally, in these studies, different features were not tied to specific temporal expectations, hindering any conclusions about the selective effects of temporal attention on non-spatial receptive fields.

Finally, a recent modelling study by Denison and colleagues (2021) developed a dynamic normalisation model of temporal attention, which successfully explains several behavioural consequences of temporal cueing. In this model, attention modulates orientation-sensitive units through gain control, providing empirically testable predictions for feature-specific modulations of temporal attention. Nevertheless, spatial uncertainty was not manipulated.

All in all, a handful of studies have suggested that temporal attention can be oriented towards expected features without spatial and motor certainty. Nevertheless, in these studies, temporal attention did not flexibly prioritise certain features over others based on changing goals. Therefore, in **Chapter 3**, I developed a task to test whether visual and auditory temporal attention can be flexibly directed to temporally expected features in the absence of spatial and action-related certainty.

1.5 Internal attention

Internal attention is the process of selectively prioritising contents in internal representations to proactively guide behaviour (Chun et al., 2011; van Ede & Nobre, 2023). To date, the vast majority of studies have considered the behavioural and neural consequences of directing internal attention to contents in working memory[6].

Working memory can be described as the maintenance and manipulation of information during brief periods and after sensory information is no longer available (Atkinson & Shiffrin, 1968; Baddeley & Hitch, 1974). Its main adaptive function is to prepare us for prospective behaviour based on past occurrences (Fuster & Bressler, 2012; Nobre & Stokes, 2019; Olivers et al., 2011; Postle, 2006; Rainer et al., 1999; van Ede, 2020; van Ede & Nobre, 2023). Internal selective attention may prioritise working-memory contents in a variety of ways, such as by selectively enhancing their quality or accessibility, or by improving their ability to guide behavioural output (Souza & Oberauer, 2016; van Ede & Nobre, 2023).

A quintessential experimental manipulation for studying internal attention is the use of *retrodictive cues* or retro-cues (Griffin & Nobre, 2003; see also Astle et al., 2012; Landman et al., 2003; Sligte et al., 2010). In Posner-like tasks, symbolic cues signal the location (or other sensory feature) of an upcoming target (pre-cue; Posner, 1980), thus encouraging a proactive prioritisation of the target's attributes before its appearance (see **Section 1.4**). In contrast, retro-cues appear during the retention period of a working-memory delay. Therefore, retro-cues prompt the selective prioritisation of contents that have already been encoded into working memory, in preparation for a prospective response.

Cueing participants to attend to an external location (external attention) or a location in working memory (internal attention) activates an overlapping network of

---

[6] See Chun et al. (2011) for an overview of internal attention to long-term memories, decisions, responses etc.

dorsal frontoparietal and occipital areas (Nobre et al., 2004; see also Bledowski et al., 2009; Esterman et al., 2009; Nee & Jonides, 2008; Tamber-Rosenau et al., 2011; Wallis et al., 2015; see **Section 1.4.1**). Interestingly, this network also includes key areas for oculomotor control (Nobre et al., 2004). Consistently, continuous behavioural metrics of the eye can track the internal prioritisation of stimulus locations (van Ede et al., 2019b, 2021; see also Spivey & Geng, 2001). This points to the involvement of the oculomotor system and its peripheral effector organs in internal attention, analogous to external attention (Deubel & Schneider, 1996).

Additional areas are also engaged during internal attention, most notably ventrolateral prefrontal regions (Lepsien et al., 2005, 2011; Nee et al., 2013; Nee & Jonides, 2008, 2009; Nelissen et al., 2013; Nobre et al., 2004; Wallis et al., 2015) and the basal ganglia (Chatham et al., 2014; Chatham & Badre, 2015; Tamber-Rosenau et al., 2011). Interestingly, these two regions have been implicated in output gating, control, task switching, and selection processes within working memory (Brady et al., 2011; Chatham et al., 2014; Chatham & Badre, 2015; Higo et al., 2011; Kuo et al., 2014; Nee et al., 2013; Nelissen et al., 2013; Richter & Yeung, 2014; Tamber-Rosenau et al., 2011).

ERPs also highlight both similarities and differences in the temporal profiles of internal and external attention. Both processes seem to modulate early posterior potentials and later frontal negativities, while retro-cues specifically modulate frontal potentials from early on (Griffin & Nobre, 2003; Kuo et al., 2009; Nobre et al., 2007).

The first NHP study contrasting external and internal attention found that internally and externally attended locations and colours were decodable in the lateral prefrontal cortex (LPFC), FEF and V4 (only location). Though preliminary, these findings are relatively consistent with the frontoparietal areas and downstream modulatory effects observed in external attention studies (see **Section 1.4**). Interestingly, however, only LPFC activity generalised to both kinds of attention, suggesting that, despite the implication of similar areas, the neuronal populations engaged in each process may differ (Panichello & Buschman, 2021).

1.5.1 Internal prioritisation of sensory contents

Regarding the modulatory effects of internal attention, univariate fMRI analyses have revealed that retro-cues activate brain regions related to prioritised locations (Kuo et al., 2014; Sligte et al., 2008, 2010) and objects (Lepsien & Nobre, 2007). Consistently, decoding approaches have identified content-specific activity during internal selection (Harrison & Tong, 2009; Lewis-Peacock et al., 2012; Serences et al., 2009). Alpha-frequency (8-12 Hz) activity over occipital areas is modulated by internal prioritisation generally (Poch et al., 2017; Schneider et al., 2015, 2016) and by location prioritisation in a spatially specific manner (De Vries et al., 2017; Myers et al., 2015; Poch et al., 2017; van Ede et al., 2017; Wallis et al., 2015; Wolff et al., 2017; see **Section 1.6.1**).

Internal attention is remarkably flexible. In contrast to the behavioural costs observed at locations (and other sensory attributes) that lie outside of the focus of external attention, selecting a sensory item in working memory does not compromise the representation of other competing items. Currently unprioritized items can be effectively selected and prioritised later (Myers et al., 2018). The capacity to flexibly prioritise, de-prioritise, and re-prioritise sensory contents depending on changing task demands and with limited behavioural costs is one of the most consistent and distinguishing features of internal attention (Christophel et al., 2018; De Vries et al., 2017, 2018; LaRocque et al., 2013; Lewis-Peacock et al., 2012; Muhle-Karbe et al., 2021; Myers et al., 2018; Rerko & Oberauer, 2013; van Ede et al., 2021; Van Moorselaar et al., 2015).

The prioritisation of internal sensory contents is also dynamic and temporally tuned. Like external attention, internal attention builds upon temporal regularities in the environment to structure the prioritisation of sensory contents accordingly. Across two studies that predictably manipulated the time at which different internal contents would be probed, both pupil size and lateralised alpha activity revealed that stimulus contrasts and locations were prioritised dynamically and at the relevant times (van Ede et al., 2017; Zokaei et al., 2019; see also Jin et al., 2020; van Loon et al., 2017). Other known ERP signatures of temporal external attention (i.e., CNV and CDA) have also been observed when internal attention is driven by temporal expectations (van Ede et al., 2020). De Vries and colleagues (2018) further revealed that during temporally predictable priority switches, occipital alpha activity was coupled with frontal theta (4-8 Hz) oscillations, which were proposed to reflect “top-down” switch coordination.

In summary, the prioritisation of sensory features in working memory is selective, proactive, flexible, dynamic, and temporally tuned. Several of its features and consequences are shared with external attention. Nevertheless, internal attention has its own set of unique and distinguishing characteristics which are becoming increasingly clear. These might reflect the different goals that internal and external attention subserve. While the former prioritises sensory contents amidst competing stimulation to create cohesive representations, the latter prioritises working-memory contents and prepares them to be imminently used to guide behaviour (Heuer et al., 2020; Myers et al., 2017; Souza & Oberauer, 2016; van Ede & Nobre, 2023).

1.5.2 Internal prioritisation of action-related contents

Internal attention has been suggested to play an essential role in preparing prospective actions, thus making working-memory contents “action-ready” (van Ede & Nobre, 2023). Consistently, in addition to prioritising sensory contents, internal attention is very effective at prioritising action-related working-memory contents (Boettcher et al., 2021; Formica et al., 2021; González-García et al., 2020; Henderson et al., 2022; Kikumoto et al., 2022; Rösner et al., 2022; Trentin et al., 2023; van Ede et al., 2019a).

In line with the activation of cortical and subcortical motor areas following retro-cues (Chatham et al., 2014; Tamber-Rosenau et al., 2011), internal selection also modulates ERPs and beta-frequency oscillatory activity linked to motor preparation (Schneider et al., 2017; see **Section 1.6.2**). Beta modulation is constrained to the hemisphere contralateral to the prospective action hand (i.e., effector-specific) when the action is imminent (van Ede et al., 2019a), and during internal prioritisation following a retro-cue (Ester & Weese, 2023). Potential actions in working memory can be prioritised even when their subsequent utilisation is uncertain (Nasrawi et al., 2023; Nasrawi & van Ede, 2022), hence proactively preparing us for different possible futures (Cisek & Kalaska, 2010).

Internal attention has been proposed to act upon working-memory contents in two separate stages. First, the cued sensory contents would be selected and prioritised and, subsequently, sensory contents would be reformatted to activate the prospective response (Myers et al., 2017). At this point, sensory-related contents may no longer be necessary, at least in tasks with low sensory demands. Consistent with this proposal, Wallis and colleagues (2015) reported the successive activation of a frontoparietal network related to alpha attenuation (i.e., sensory prioritisation), followed by a cingulo-opercular network proposed to reflect the motor transformation step. Several other studies have found that sensory codes are converted into motor codes in working memory when the subsequent response is certain (González-García et al., 2020; Henderson et al., 2022; Kikumoto et al., 2022; Panichello & Buschman, 2021).

In contrast to the intuition of serial sensory selection followed by motor transformation, recent studies suggest that sensory and motor modulations do not necessarily unfold in a serial, orderly fashion. A recent study which independently manipulated location and action-related content selection revealed that the prioritisation of item locations and prospective actions unfolded in parallel (van Ede et al., 2019a). Consistently, a different study found that, when available, action-related contents could be selected at very early stages of processing, specifically, during encoding of visual items into working memory (Boettcher et al., 2021). The same study additionally revealed that action selection did not build up slowly over the working-memory retention period, as it may have been predicted from a gradual sensory-to-motor code transformation. Instead, action contents were prioritised at encoding, seconds before they would become relevant, then re-prioritised before the imminent response.

On the whole, sensory contents in working memory are flexibly prioritised depending on changing goals. Moreover, motor prioritisation in working memory is a key element of the pragmatic nature of internal attention. Additionally, the prioritisation of sensory and action-related contents in working memory is not always serial. However, much remains to be learned about whether and how sensory- and action-related contents that co-exist in working memory are flexibly and dynamically prioritised according to changing goals. This is the question that motivates **Chapter 4** of this thesis. To address it, I rely on continuous metrics of neural activity (with EEG) and behaviour (with eye-tracking).

1.6 TIME COURSES OF SENSORY- AND ACTION-RELATED PRIORITISATION

Frequency-specific patterns of neural activity, often referred to as neural oscillations, are ubiquitous in the brain and have been suggested to play key functional roles in multiple cognitive processes (Buzsáki, 2006; Fries, 2005; Siegel et al., 2012; Thut et al., 2012; Varela et al., 2001). In **Chapter 4** of this thesis, I use alpha-frequency activity modulations and horizontal gaze position as markers of location prioritisation in working memory and mu-beta-frequency activity as a proxy for selection of prospective hand actions.

1.6.1 Alpha-frequency activity

Neural oscillations in the alpha-frequency band (~8-12 Hz) were the first properties noted in the ongoing brain activity when the EEG method was developed (Berger, 1929). Alpha oscillations have long been linked with the gating of sensory signals (Adrian & Matthews, 1934; Berger, 1929; Hari & Salmelin, 1997). A relative reduction in alpha-frequency activity is related to the anticipatory allocation of external attention to visual features (Foxe et al., 1998; Thut et al., 2006; Worden et al., 2000). Similarly, directing internal attention to sensory features is accompanied by a relative attenuation in alpha-frequency activity in related visual areas (Mok et al., 2016; Myers et al., 2015; Poch et al., 2014, 2017; Schneider et al., 2015, 2016; van Ede, 2018; Wallis et al., 2015). The extent of alpha reduction has been correlated with behaviour both in internal and external attention (Thut et al., 2006; van Driel et al., 2017; van Ede et al., 2017), and stimulation studies point to a causal functional involvement of alpha activity in attention (Clayton et al., 2019; Romei et al., 2010; Sauseng et al., 2009; Spaak et al., 2014).

When external or internal attention is directed to a specific location, alpha activity is relatively attenuated over contralateral occipital regions (Myers et al., 2015; Poch et al., 2017; Schneider et al., 2015, 2016; Wildegger et al., 2017), a property of alpha which will be harnessed in **Chapter 4** of this thesis. Content-specific activity patterns can be decoded from occipital alpha (de Vries et al., 2019; Foster et al., 2017; van Moorselaar & Slagter, 2019) and alpha activity reductions have also been observed in invasive recordings following attention cues (e.g., Lima et al., 2011). Suppression in alpha activity is thought to reflect an increase in excitability of the underlying neuronal populations (Iemi et al., 2022; Jensen & Mazaheri, 2010; Klimesch et al., 2007) and the tuning of sensory neurons to the attended feature (Klimesch, 2012; Treue & Martínez Trujillo, 1999).

In the context of internal attention, Fukuda and colleagues (2015, 2016) have suggested that the sustained attenuation of alpha activity observed during selection of a cued item may be different to the more transient, lateralised alpha suppression that is specific to selected locations. Consistent with this, lateralised alpha modulations correlate with improved performance when they are brief (Mok et al., 2016), whereas general alpha attenuation facilitates behaviour more strongly when it is longer-lived (De Vries et al., 2020; Fukuda et al., 2015, 2016; van Ede, 2018). This, together with several other pieces of evidence, suggest that the alpha-frequency modulations recorded with non-invasive human neurophysiology may not represent a unitary phenomenon.

1.6.2 Mu-beta-frequency activity

Another prominent class of frequency-specific activity occurs in the mu-beta band (mu: 8-12 Hz; beta: 13-30 Hz; Jasper & Penfield, 1949; Jenkinson & Brown, 2011; Kilavik et al., 2013; Salmelin & Hari, 1994; Schoffelen et al., 2005). Mu-beta activity is usually recorded over frontocentral sensors in EEG and MEG (Pfurtscheller et al., 1996). Mu-beta modulations covary with movements, showing an initial desynchronisation upon movement initiation and a subsequent re-bound synchronisation following movement termination (Pfurtscheller et al., 1996). In addition to movement execution, mu-beta activity is tightly linked with delayed action preparation (Kaiser et al., 2001; Pfurtscheller & Berghold, 1989). Mu-beta activity over contralateral central sensors is reduced in preparation for a hand action (Kaiser et al., 2001; Leocani et al., 1997; Pfurtscheller et al., 2000). Furthermore, the magnitude of preparatory mu-beta modulation correlates with improved performance (Androulidakis et al., 2007). Mu and beta rhythms have been suggested to have distinct anatomical origins and to reflect the engagement of different brain networks (Ronnqvist et al., 2013; Salmelin et al., 1995; Salmelin & Hari, 1994). Nevertheless, they are both modulated by motor preparation and, therefore, they will be considered jointly in **Chapter 4** of this thesis.

Mu-beta activity has been suggested to reflect the engagement of cortico-striatal-thalamic circuits (e.g., Klostermann et al., 2007). Mu-beta-frequency activity recorded over the motor cortex seems to oscillate in phase with muscular activity in the contralateral hand, a phenomenon referred to as cortico-muscular coherence (Fries, 2005).

Mu-beta-frequency activity is also thought to index the engagement of top-down control processes in external attention and other cognitive functions (Buschman & Miller, 2007; Engel & Fries, 2010; Fiebelkorn et al., 2018; Gregoriou et al., 2012; van Ede et al., 2011). Beta- (13-30 Hz) and gamma- (>30 Hz) frequency activity have further been proposed to play a key role in working memory (for review see Lundqvist et al., 2024). Recent studies have questioned the oscillatory nature of beta-frequency activity by highlighting its short-lived temporal profile. Transient increases in beta-activity power (beta bursts) seem to correlate with the relevant cognitive processes (Echeverria-Altuna et al., 2022; Feingold et al., 2015; Jones, 2016; Lundqvist et al., 2016; Quinn et al., 2019; Shin et al., 2017).

Interestingly, both alpha- and mu-beta-activity are modulated by external temporal attention (Heideman et al., 2018b; Rohenkohl & Nobre, 2011). In internal attention, analogous alpha modulations have been observed during temporally predictable prioritisation (van Ede et al., 2017). The modulation of mu-beta activity as a function of the prioritisation of prospective actions in working memory according to temporal expectations had not yet been tested until **Chapter 4**.

1.6.3 Microsaccades

Microsaccades are small (<1 DVA) eye movements that happen involuntarily when holding fixation (Martinez-Conde et al., 2004; Rolfs, 2009; Rucci & Poletti, 2015). They have been suggested to reflect shifts in endogenous spatial attention (Yuval-Greenberg et al., 2014), yet they do not seem necessary for attentional shifts to occur (Liu et al., 2022; Poletti et al., 2017). Interestingly, microsaccade suppression has been observed around the time of temporally expected visual (Denison et al., 2019) and auditory (Abeles et al., 2020) stimuli.

Recently, the prioritisation of location-related working-memory contents has been linked to spatially specific biases in microsaccades towards the prioritised location (Draschkow et al., 2022; Gresch et al., 2024; van Ede et al., 2019b). Interestingly, these biases are observed even when space is not a relevant feature for the task (de Vries & van Ede, 2024; van Ede et al., 2019b). These biases suggest that internal attention builds upon the neural architecture of external attention, which is tightly linked with oculomotor control (Rizzolatti et al., 1987).

Interestingly, tracking small movements in gaze position in a task requiring successive reports of two spatially arranged items revealed that switching from the first to the second item location occurred, on average, before the end of the first item report (van Ede et al., 2021). This shows the dynamic nature of sensory prioritisation in working memory. Moreover, it highlights the temporal resolution and sensitivity of gaze position as a proxy of the dynamic prioritisation of working-memory contents. In **Chapter 4**, I harness these properties to study visual and auditory internal attention.

1.7 AIMS OF THE THESIS

My doctoral research investigates how perception and attention are tuned to different temporal structures in the environment. I use the term temporal structures to refer to regularities in stimulus features (feature regularities) and regularities in temporal intervals between events (temporal regularities).

In **Chapter 2**, I investigate whether feature regularities which unfold over different timescales jointly modulate ongoing perception, as indexed by perceptual biases. Specifically, I investigate the interrelations between perceptual biases emerging from exposure to medium-term feature regularities and serial biases between temporally adjacent events. Across three experiments, the predictability and relevance of the regular feature is manipulated to investigate how guidance signals modulate perception.

In **Chapter 3**, I turn to studying the temporal orienting of visual and auditory attention to external events. Specifically, I develop a task design that concomitantly encourages the incidental learning of temporal regularities and the flexible orienting of temporal attention as a function of changing goals. In three experiments, the temporal orienting of attention to temporally expected visual and auditory features unfolds under uncertainty about stimulus location and required response.

Finally, in **Chapter 4** I investigate the temporal tuning of internal sensory- (visual and auditory) and action-related content prioritisation. I harness oscillatory EEG activity and eye-tracking to follow the time courses of visual and action-related content prioritisation based on external cues and internally driven temporal expectations. Moreover, I interrogate the flexible and temporally tuned nature of auditory internal attention.

The theme of the present thesis has a clear temporal undercurrent. It investigates the behavioural consequences of feature regularities across timescales (**Chapter 2**), and how temporal regularities sculpt external (**Chapter 3**) and internal (**Chapter 4**) attention. Time is also pervasive in the designs and methodologies of this thesis. In addition to using temporally resolved physiological markers, the task designs presented here are driven by the common aim of assimilating the temporal dimension. The task in **Chapter 2** is a continuous stream of stimuli in which regularities unfold over different timescales. **Chapter 3** uses extended and dynamic stimuli to encourage the incidental learning of feature-temporal regularities over time, and **Chapter 4** investigates the effects of the same temporal expectations on distinct sensory and action systems.

Another recurrent motif of this thesis is the manipulation of guidance signals such as expectations and goals to investigate how they jointly guide perception and attention. In **Chapter 2**, the predictability and relevance of feature regularities changes across experiments. **Chapter 3** explores the interplay between incidentally acquired expectations and endogenously driven goals. Finally, **Chapter 4** arbitrates between expectations that are called upon by explicit cues and the internal monitoring of task-goals which change predictably over time.

The completed studies recurrently consider the action-oriented nature of perception and attention with questions like the following. Can regularities bias perception when they do not require active task-engagement (**Chapter 2**)? Can temporal expectations orient attention without motor certainty (**Chapter 3**)? How does internal attention prioritise, de-prioritise, and re-prioritise action-related working-memory contents dynamically (**Chapter 4**)? They additionally consider how time interacts with space and other sensory features.

Finally, a common effort of this thesis is translating between sensory modalities (vision and audition) to test the generalisability of the present findings between sensory systems which profoundly differ in their temporal structuring.

2 Feature regularities across timescales jointly modulate perception

2.1 Abstract

Ongoing perception is shaped by regularities at multiple timescales. Recent studies point to concurrent and interactive modulations of perception by temporal adjacency between events and by medium-term regularities in the context of an ongoing task. Nevertheless, it remains unknown whether and how perception is jointly biased by the immediate past and medium-term feature regularities which are also predictable in the short-term. To address this, I investigated perceptual biases in orientation-reproduction tasks manipulating medium-term task statistics. One orientation repeated more frequently among other randomly oriented stimuli. Across three experiments, reports of randomly oriented targets were consistently biased away from the *repeated* orientation (repetition bias). This repetition bias occurred regardless of the predictability, explicit knowledge, and relevance of the repeated orientation. Finally, the repeated orientation biased subsequent orientation reports to a larger extent than randomly oriented targets, suggesting combined effects of short- and medium-term feature statistics. The present findings add to emerging evidence suggesting that statistical regularities across different timescales concurrently shape perception.

2.2 INTRODUCTION

The external world is highly structured. These regularities give rise to expectations about upcoming events which, in turn, facilitate behaviour and modulate perception (e.g., de Lange et al., 2018; Nobre & van Ede, 2018, 2023; Rosen, 2012). Exposure to stimulus regularities results in perceptual biases whereby random features are reported as systematically biased towards (more similar) or away (more dissimilar) from the regularly occurring feature (de Lange et al., 2018; Seriès & Seitz, 2013).

Regularities unfolding over different timescales can jointly influence perception (Seriès & Seitz, 2013). At the lengthy span of long-term learning, a lifetime of exposure to cardinal orientations results in systematic perceptual biases towards such orientations (Gibson & Radner, 1937; Girshick et al., 2011; Xu et al., 2006). Relatedly, exposure to stimuli with a specific feature distribution biases feature reports towards the mean of the distribution (Hollingworth, 1910; Huttenlocher et al., 2000; Jazayeri & Shadlen, 2010).

Stimulus statistics also regularly emerge at mid-range timescales within the context of an ongoing task (medium-term regularities) and can improve task performance (Chun & Jiang, 1998; Schapiro & Turk-Browne, 2015). In addition to facilitating behaviour, exposure to feature regularities (e.g., repeated motion direction) over tens of minutes is known to bias perception towards the repeated motion direction (Chalk et al., 2010; Gekas et al., 2013, 2015; see also Kok et al., 2013; Scotti et al., 2021; Sotiropoulos et al., 2011).

Interestingly, similar perceptual biases have been reported between neighbouring events, an effect referred to as serial dependence or serial bias. Temporal adjacency between visual events results in perceptual biases whereby feature reports of the stimulus in trial N are biased towards or away from the feature in trial N-1 (e.g., Cicchini et al., 2014, 2024; Fischer & Whitney, 2014; Manassi et al., 2023; Pascucci et al., 2023; Thompson & Burr, 2009). Serial biases have been found across multiple stimulus features, task demands, sensory domains, and species (for recent reviews see Cicchini et al., 2024; Manassi et al., 2023; Pascucci et al., 2023).

Given their ubiquitous nature, serial biases have been proposed to play a functional role in perception. Attractive biases may promote visual stability (Cicchini et al., 2018; Czoschke et al., 2019; Fischer et al., 2020; Fischer & Whitney, 2014; Manassi & Whitney, 2022); repulsive biases may increase sensitivity to change (Clifford, 2002; Clifford et al., 2007; Kohn, 2007; Thompson & Burr, 2009; Weber et al., 2019; Webster, 2015). Broadly, they have been suggested to reflect a process of adaptation to the statistics of the visual environment (i.e., Barbosa & Compte, 2020; Cicchini et al., 2018; Clifford et al., 2007; Felsen et al., 2005; Fischer & Whitney, 2014; Kiyonaga et al., 2017; Panichello et al., 2019; van Bergen & Jehee, 2019; Weber et al., 2019).

Nevertheless, most studies of serial biases have used stimuli from uniform (random) feature distributions and, therefore, feature regularities were absent. Recently, some studies have begun investigating the effects of medium-term feature regularities on serial biases. For example, exposure to facial attributes considered stable (gender) vs changeable (expression) was reported to result in serial biases with opposite directions (Taubert et al., 2016). This and other studies have shown that exposure to medium-term feature regularities modulates serial biases (see also Blondé et al., 2023; Chopin & Mamassian, 2012; Gekas et al., 2019; Panichello et al., 2019).

In a similar vein, serial biases seem to interact with perceptual biases resulting from exposure to a consistent feature distribution, such as the central tendency effect (Bae, 2024; Chopin & Mamassian, 2012; Gekas et al., 2019; Glasauer & Shi, 2022; but see Cicchini et al., 2022; Galluzzi et al., 2022; Lieder et al., 2019; Saarela et al., 2023). Interestingly, inactivation of the PPC in rodents resulted in the simultaneous ablation of serial biases and the contraction bias, towards the average feature of multiple past stimuli (Akrami et al., 2018). Furthermore, the behavioural effects of serial dependence are better explained by models which also include parameters describing medium-term statistical regularities (Chopin & Mamassian, 2012; Gekas et al., 2019; Glasauer & Shi, 2022; Kalm & Norris, 2018; Tong & Dubé, 2022; van Bergen & Jehee, 2019). Finally, serial biases and perceptual biases arising from long- or medium-term exposure to statistical regularities have been successfully described within the same Bayesian framework (e.g., Hahn & Wei, 2024).

Together, these findings point to close but relatively unexplored relations between serial biases and perceptual biases related to regularities across different timescales. Specifically, it remains unknown whether and how perception is jointly biased by the immediate past (serial bias) and by shorter- (predictive relations between neighbouring events) and longer-term (prolonged exposure to regularities) regularities in the environment.

Here, an orientation-report task was used to test whether blocked exposure to a *repeated* stimulus feature systematically influenced task performance across three experiments. Specifically, I was interested in whether exposure to this *repeated* orientation would bias other orientation reports. Additionally, I investigated whether this bias would be modulated by the behavioural relevance of the *repeated* feature, as manipulated by changing the explicit predictability of the *repeated* feature (Experiments 1 and 2) and the requirement to respond to it (Experiment 3). Moreover, I tested whether features which predicted the appearance of the repeated stimulus would be differentially biased. Finally, I examined whether the feature regularity resulted in biases above and beyond the more typically studied biases of the immediate past (serial bias; hereafter referred to as retrospective bias).

To foreshadow the results, random orientations were reported as systematically more dissimilar to the *repeated* orientation across three experiments. This *repetition* bias occurred regardless of whether the *repeated* orientation was explicitly known and predicted by participants (Experiments 1 and 2) or was never reported by participants (Experiment 3). Interestingly, this *repetition* bias was not consistently different for stimuli which predicted the forthcoming *repeated* orientation. Finally, the *retrospective* bias induced by the *repeated* orientation on subsequent orientation reports was stronger than the *retrospective* bias of other, randomly oriented gratings.

2.3 EXPERIMENT 1

2.3.1 Methods

2.3.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R73580/RE001). In Experiment 1, 54 participants were recruited through the Prolific Academic platform (https://www.prolific.co). Participants were pre-screened to ensure they were aged 18 to 40, fluent in English, had normal or corrected-to-normal eyesight, and fulfilled specific participation requirements in Prolific Academic. Study inclusion required an approval rate above 95% and participation in at least ten prior studies. Participants were paid at a rate of £10 per hour, and those whose performance accuracy was above 95% received an additional monetary reward scaling from £0.01 (95%) to £5 (100%). All participants provided informed consent prior to beginning the study. The sample size was based on an initial power analysis in G*Power (Faul et al., 2007) that aimed at detecting medium-sized effects ($d = 0.5$, $\alpha = 0.05$, $1-\beta = 0.95$) and on other studies hosted in the same server, which reported performance biases in continuous orientation reports (e.g., Gresch et al., 2021).

Due to variable quality in online experiments (Sauter et al., 2020), strict exclusion criteria were pre-defined and used. Data from participants were excluded from further analyses if participants' performance accuracy was below 50%, if they did not respond to more than 20% of trials, if they had a mean RT above 3 SDs from the cross-participant average, or if they had a mean accuracy below 3 SDs from the cross-participant average. Data from two participants were excluded from further analyses based on these criteria. Additionally, a pre-defined trial-removal procedure helped to identify the proportion of "bad" trials per participant (see **Data analysis** for details). A further two participants were excluded from subsequent analyses because their proportion of "bad" trials was higher than 3 SDs from the mean proportion of "bad" trials across participants. Finally, data from one participant were excluded from further analyses due to inaccurate reproduction of the *repeated* orientation at the end of the block (see **Experimental procedure and stimuli** for details). A total of 5 participants were excluded from further analyses, leaving a final sample of 49 participants (mean age: 23.86; age range: 18-39; age SD: 5.81; 17 female, 31 male, and 1 preferred not to say; 3 left-handed).

2.3.1.2 Experimental procedure and stimuli

The experimental script was generated using PsychoPy (PsychoPy Builder v2021.1.4; Peirce et al., 2019) and hosted online through Pavlovia (https://pavlovia.org/; Sauter et al., 2020). Participants completed the study on their personal computers or laptops using either Mozilla Firefox or Google Chrome and were asked to keep 60 cm away from their screens. They were not allowed to participate in the study using phones or tablets. At the beginning of the experiment, participants were asked to place a standard-sized card against the screen and scale the image of a credit card on the screen until it matched the physical one. The procedure served to estimate the resolution of the computer screen (Li et al., 2020). The ratio between the card image width (pixels) and the actual card width (cm) provided the pixel density (pixel per cm) per participant. Together, this value and the recommended distance from the screen (60 cm) helped estimate the DVA of the task stimuli.

Participants performed an orientation report task on a series of centrally presented tilted Gabor patches. After each stimulus, they moved a dial to match the orientation of the Gabor (**Figure 2.1a**).

At the beginning of each trial, a clearly visible Gabor (a sinusoidal grating with a Gaussian envelope) with a diameter of 7 DVA, a spatial frequency of 2 cycles per degree (CPD), and a contrast of 0.5, was displayed in the centre of the screen for 100 ms. Gabor disappearance was followed by a delay period of 650 ms, during which a fixation circle was shown centrally (1 DVA diameter). After the delay, the probe appeared: a centrally displayed dial with a diameter of 5.7 DVA and two parallel rectangular markers along opposite sides of the circle. Participants adjusted the orientation of the dial (1.4 DVA) to match the angle of the Gabor (**Figure 2.1a**). Specifically, when participants moved the mouse, the rectangular markers drifted around the perimeter of the dial in the direction of the cursor's location in steps of 1°. Participants clicked the mouse when they considered that the dial matched the Gabor's orientation to confirm their response. In each trial, the dial's starting orientation was randomly chosen from a uniform distribution (1-180°) and the cursor was invisible to the participants. Following probe appearance, participants had a maximum of 2000 ms to reproduce the orientation of the Gabor. Before progressing to the next stimulus, they were always required to wait until the end of this 2000 ms period even if they confirmed their orientation report earlier. This ensured that the time between perceptual events remained constant and independent from trial-to-trial variations in response times. After an ITI of 500 ms, a new trial began.

The Gabor patches used in this task varied across two features: colour and orientation. The colour of each Gabor patch corresponded to one out of six possible colours equidistantly spaced in the CIELab colour space (CIE, 2004; orange: #D55E00, blue: #0072B2, pink: #CC79A7, brown: #9C755F, green: #009E73).

For each participant, one of the six possible colours was randomly designated as the *repeated* colour for the duration of the study. Out of the five remaining colours, an additional colour was randomly selected as the *cueing* colour. The remaining four colours were considered *random*. In most trials, the colour of the Gabor was chosen equiprobably out of five possible colours (the *cueing* colour and the four *random* colours). Importantly, trials in which the *cueing* colour was displayed were always followed by trials with a Gabor with the *repeated* colour. Thus, if the Gabor with the *cueing* colour was displayed in one trial (N), it was fully predictive (100%) of the appearance of the *repeated* colour in the subsequent trial (N+1).

The to-be-reported orientation was chosen randomly from a uniform distribution ranging from 1° to 180° for all Gabors except those with the *repeated* colour (1/6th of trials). The orientation of the Gabor associated with the *repeated* colour was constant in each of the 10 blocks of the task, but it changed between blocks. Specifically, in each block, the *repeated* orientation was chosen randomly from one out of ten possible orientation bins spanning 180° (1-18°; 18-36°, 36-54°, 72-54°, 72-90°, 90-108°, 108-126°, 126-144°, 144-162°, 162-180°). The order of the orientation bins was randomised such that the target orientation in any given block was chosen from a random bin that was never sampled again.

As the main manipulation of medium-term feature statistics, the orientation of Gabors with the *repeated* colour remained consistent for the duration of a block. Importantly, at the beginning of each block, participants were explicitly informed about the predictive relation between the *cueing* and the *repeated* Gabors. Additionally, they were shown the orientation of the *repeated* Gabor, were asked to remember it, and were prompted to reproduce it at the end of each block. Participants who reproduced the *repeated* Gabor's orientation at the end of the block with an error higher than three SDs from the cross-participant average error were excluded from further analyses (n = 1).

All other participants successfully remembered the *repeated* orientations and their average end-of-block report error was 10.47° (SD: 8.59°). At the end of the task, participants were asked about the colour contingency between the *cueing* and the *repeated* Gabors. All participants correctly identified the colour of the *repeated* Gabor as the colour that followed the *cueing* Gabor. This confirmed that participants held the *repeated* orientation and *cueing* contingency in memory.

Before beginning the experiment, participants received instructions about the task procedure. They were encouraged to report the orientation of all Gabors as quickly and as accurately as possible. The task was divided into 10 blocks, each containing 100 trials and lasting 5.42 minutes. Thus, the study lasted a total of ~1 h. Before the first block, participants practised the orientation-report procedure for an unlimited amount of time and were asked to complete 8 practice trials. Between blocks, participants were provided with feedback about their mean accuracy on that block. They were informed about the percentage of trials without a response to encourage them to respond to all targets as accurately as possible. Participants were instructed to rest between blocks.

2.3.1.3 Data analysis

All data analyses were performed using the R statistical programming language (version 4.2.1; R Core Team, 2021) and R studio (version RStudio 2022.07.1; RStudio Team, 2022). The following trials were excluded from subsequent analyses: trials without a response, trials with responses faster than 100 ms, trials with responses slower than three times the SD of the average RT for each participant, and trials with report errors higher than three times the SD of the average report error for each participant. After cleaning, an average of 1.99% (SD: 1.24%) trials were removed in the final sample of participants (n = 49). The variables of interest were report error (the absolute deviation from target orientation to reported orientation) and reaction time (RT; time from probe onset to report confirmation) in each trial.

I investigated whether participants' orientation reports were systematically biased by two possible inducer orientations: the orientation of the *repeated* Gabor (*repetition* bias and *prospective* bias) and the orientation of the Gabor from the previous trial (*retrospective* bias). The *repetition* bias referred to the bias exerted by *repeated* Gabor (inducer) on all *random* orientation reports. The *prospective* bias captured the bias exerted by the *repeated* Gabor (inducer) on the *cueing* Gabors that immediately preceded and predicted the *repeated* Gabors. The *retrospective* bias was quantified as the bias exerted by any Gabor on trial N (inducer) on the orientation report of the *random* Gabor on trial N+1. Biases in orientation reports were calculated by estimating response-bias curves, which represent the extent to which participants' orientation reports deviated from the target orientation and were shifted towards or away from the inducer orientation.

To account for general, unspecific response biases, each participants' average reproduction error across all conditions was subtracted from the trial-wise reproduction error (see also Gresch et al., 2021; Hajonides et al., 2023). *Repetition, prospective,* and *retrospective* biases were quantified as the circular distance between the reproduced orientation in a given trial and the original target orientation on that trial as a function of the circular distance between the target orientation and the inducer orientation. Following subtraction of the target and inducer orientations, the angular differences were mapped between -90° and 90°. Subsequently, the circular differences between the target and inducer orientations were binned into 54 overlapping bins (size: 20°). The report error was calculated for each bin using a moving-window procedure with a step size of 3°. The angular differences were wrapped around, thus ensuring that a constant number of trials was used to calculate response bias in each bin. This yielded one value of response bias per orientation bin as a function of the angular difference between the target and the inducer orientation: the response-bias curve. Response-bias curves were calculated per participant and per condition and subsequently averaged across participants for each condition of interest. A matching sign between the reproduction error and the angular difference between the target and the inducer indicated the presence of a positive (attractive) bias, whereas a differing sign between both pointed to a negative (repulsive) bias (Fischer & Whitney, 2014).

To quantify the bias induced by the *repeated* Gabor on all *random* Gabor reports (i.e., *repetition* bias), the trials immediately following a *repeated* Gabor were excluded to minimise the influence of *retrospective* biases induced by the *repeated* Gabor on the calculation of the *repetition* bias. Similarly, to calculate the bias induced by the *repeated* Gabor on *cueing* Gabors (*prospective* bias), *cueing* Gabors that immediately followed a *repeated* Gabor were excluded.

Retrospective biases were calculated as those induced by the Gabor of the preceding trial (N-1) on the orientation report of the current trial (N; Fischer & Whitney, 2014). These were separated into the *random retrospective* bias – exerted by any *random* Gabor on any subsequent *random* Gabor – and the *repetition retrospective* bias – the bias of the *repeated* Gabor on subsequent *random* orientation reports.

All bias curve calculations excluded trials identified as "bad" (see above for details). Moreover, the number of trials used to calculate the response biases per condition was matched to ensure comparable variance across conditions. Matching was achieved by randomly subsampling trials in the condition with the most trials until it matched the condition with the least trials. This resulted in an average of 511.81 trials (SD: 25.9) per participant for calculating the *repetition* bias curve and the *shuffled control* (see **Statistical testing** for details). An average of 128.43 trials (SD: 7.6) was used to calculate the *repetition retrospective* bias and 129.41 trials (SD: 6.51) for the *random retrospective* bias. For calculating the *prospective* bias, the average distance from a *repeated* Gabor to subsequent *random* Gabors and *cueing* Gabors was matched per participant by random trial sampling. This ensured that any potential lingering bias of the *repeated* Gabor was matched when comparing the *prospective* bias with the *repetition* bias. On average, 118.41 trials (SD: 7.67) per participant were used to calculate the *prospective* bias and its corresponding control *repetition* bias.

2.3.1.4 Statistical testing

The statistical significance of the variables of interest across participants (report error and RT) was tested using repeated-measures ANOVA with condition (*cueing*, *repeated*, and *random*) as a factor. η^2 was the metric of effect size and the within-subject SEM was quantified using the normalised data (Morey, 2008). When relevant, the p-values of the ANOVAs were displayed as corrected by the Greenhouse-Geisser Correction for Sphericity (p_{GG}). Post-hoc comparisons were performed using two-sided paired-samples Student's t-tests and Cohen's d measured effect size. Following unplanned post-hoc comparisons, the resulting p-values were corrected for multiple comparisons using the Bonferroni method.

The statistical significance of the *repetition* bias was tested against a well-matched condition. To this end, a null condition was generated which accounted for potential artefacts in bias curve estimation when using repeated orientations as inducers. The 10 *repeated* orientations chosen across blocks were shuffled for each participant. For each block, the reproduction bias to the *repeated* orientation from a different block was calculated (**Figure 2.1a**).

Subsequently, the statistical significance of the difference between the *repetition* bias and the *shuffled control* condition across participants was evaluated using cluster-based permutation testing (Maris & Oostenveld, 2007). First, a mass-univariate t-test (two-sided, alpha = .05) was performed on the group-level bias curves, and cluster statistics were calculated. Then, the bias curves across the two conditions of interest were randomly permuted (sign-flipped) 10,000 times per participant, defining the null hypothesis. The summary statistics of the largest clusters of the null hypothesis were compared with the observed data, thus generating distributions of summary cluster statistics and circumventing the multiple comparisons problem (Maris & Oostenveld, 2007). The same approach assessed the difference between the *prospective* bias and the *repetition* bias and between the *repetition retrospective* bias and the *random retrospective* bias.

As a complementary analysis, the AUC of the response-bias curves of interest was compared: *repetition* bias vs *shuffled control, prospective* bias vs *repetition* bias*, repetition retrospective* bias vs *random retrospective* bias. To this end, bias curves for each condition were integrated separately for negative and positive target-to-inducer angles, sign-matched and compared between the conditions of interest using paired-samples t-tests.

All statistical tests were two-sided, and the error bars and the shaded areas depicted in all figures correspond to the SEM. Following the American Psychological Association (APA) conventions, statistically significant differences between conditions are denoted by asterisks on all figures. The *ggplot2* R package (version 3.3.6; Wickham, 2009) was used for plotting.

2.3.2 Results

In this experiment, the primary interest was assessing the influence of medium-term feature regularities on participants' general performance and perceptual biases. The key manipulation was the presence of a *repeated* Gabor whose orientation was displayed more frequently (1/6th of trials) than any other orientation within a block. Importantly, trials with a *repeated* Gabor were predictable, always appearing following a *cueing* Gabor, with a constant colour.

2.3.2.1 General performance

When comparing the predefined behavioural variables-of-interest (report error and RT) in response to *random*, *cueing*, and *repeated* Gabors with a repeated-measures ANOVA, a main effect of condition on report error was found ($F(1,96) = 7.92$, $^{**}p_{GG} = .004$, $\eta^2 = .012$; **Figure 2.1b**). Post-hoc t-tests revealed that participants were consistently more accurate at reporting the tilt of *repeated* Gabors (M_{rep}: 6.47°, SD_{rep}: 2.68°) compared to *random* Gabors (M_{rand}: 7.46°, SD_{rand}: 2.91°; $t(48) = -3.27$, $^{**}p = .002$, $d = .47$). Additionally, *repeated* Gabors were reproduced with a lower report error than *cueing* Gabors ($t(48) = -2.43$, $^{*}p = .02$, $d = .35$). Finally, there was a trend towards a lower report error to *cueing* vs *random* Gabors (M_{cue}: 7.31°, SD_{cue}: 2.87°; $t(48) = -1.97$, $p = .06$, $d = .28$).

Another ANOVA revealed a main effect of condition on reaction time ($F(1,96) = 25.96$, $^{***}p_{GG} < .001$, $\eta^2 = .005$; **Figure 2.1c**), whereby participants were slower at reporting *repeated* (M_{rep}: 588.78 ms, SD_{rep}: 235.47 ms) than *random* Gabors (M_{rand}: 551.28 ms, SD_{rand}: 224.6 ms; $t(48) = 5.7$, $^{***}p < .001$, $d = .81$) and *cueing* (M_{cue}: 557.83 ms, SD_{cue}: 219.74 ms) vs *random* Gabors ($t(48) = 4.76$, $^{***}p < .001$, $d = .68$). Moreover, *cueing* Gabors were reported more slowly than *repeated* Gabors ($t(48) = 4.77$, $^{***}p < .001$, $d = .68$). Together with the report error, this pattern of findings pointed to a general influence of the *repeated* Gabor and the *cueing-repeated* contingency on participants' performance. This result additionally pointed to a speed-accuracy trade-off in participants' responses to *repeated* Gabors with more accurate orientation reports at the expense of slower RTs.

At the end of each block, participants were asked to reproduce the orientation of the *repeated* Gabor. Their report error was 10.47° (SD: 8.59°), suggesting they successfully remembered the *repeated* orientations. Moreover, all participants correctly reported the contingency between the *cueing* and the *repeated* Gabor colour at the end of the task.

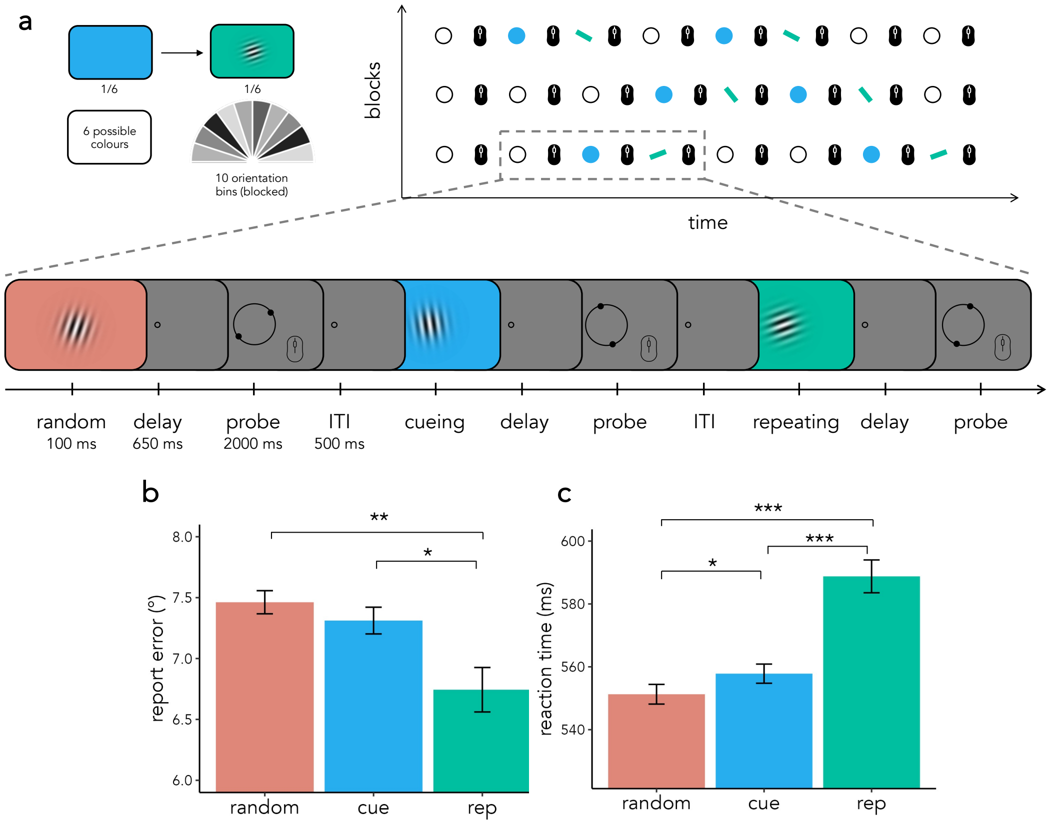


Figure 2.1. Experiment 1: task design and general performance. a) Trial schematic. In each trial, participants reported the orientation of a target Gabor coloured in one of six possible colours. For each participant, one of the colours was randomly selected as the *repeated* colour and another as the *cueing* colour. The colour of the target in each trial was chosen randomly out of five possible colours (the *cueing* colour and the four remaining *random* colours) and its orientation was chosen equiprobably from 1-180°. When the *cueing* colour was chosen in trial N-1, the following trial (N) would display a target with the *repeated* colour. Moreover, targets with the *repeated* colour had a constant orientation within a block chosen out of 10 non-repeating orientation bins spanning 180°. The orientation of the *repeated* Gabor and the predictive relation between the *cueing* colour and the *repeated* Gabor was explicitly disclosed to participants at the beginning of each block. b) Mean report error (°) to *random*, *cueing*, and *repeated* Gabors. c) Mean reaction time (ms) to *random*, *cueing*, and *repeated* Gabors. Error bars depict the SEM and asterisks denote statistically significant differences following relevant statistical tests.

2.3.2.2 Perceptual biases

The presence of a *repeated* orientation was hypothesised to result in systematic perceptual biases on other orientation reports. To test this, the bias induced by the *repeated* Gabor on *random* orientation reports was calculated (see **Data analysis and statistical testing**). Cluster-based permutation analyses (Maris & Oostenveld, 2007) and a t-test between the AUC of the *repetition* bias curve (M_{rep}: 24.02, SD_{rep}: 86.77) and the *shuffled control* bias curve (M_{con}: -27.65, SD_{con}: 81.55) revealed that the *repeated* orientation exerted a repulsive bias on *random* Gabor reports (**Figure 2.2a,b**; left to right; *cluster 1* (-41 to -8): ***p < .001, *cluster 2* (10 to 52): ***p < .001; t(48) = 5.9, ***p < .001, d = .84). This indicated that a frequently presented orientation resulted in a general bias (*repetition* bias), whereby orientation reports of *random* Gabors were systematically repelled away from the *repeated* feature.

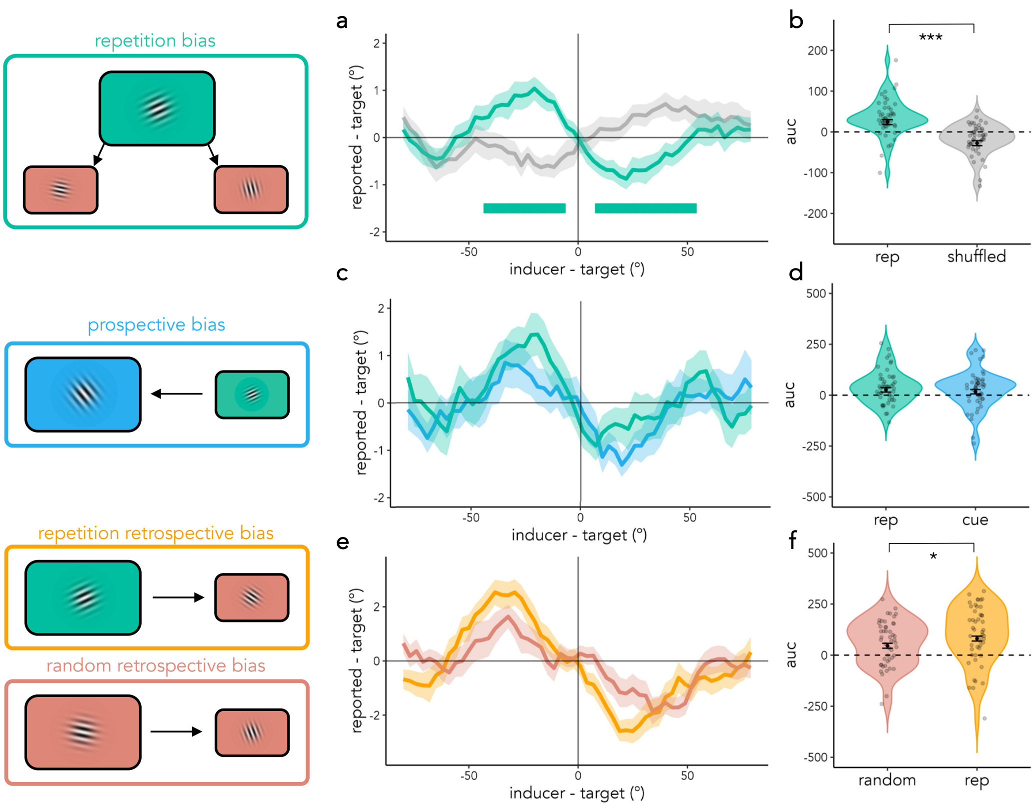


Figure 2.2. Experiment 1: repetition bias, prospective bias, and retrospective biases. a) Average response bias relative to the angular difference between *random* Gabors and the *repeated* orientation (*repetition* bias; green) and between *random* Gabors and the *shuffled repeated* orientation (*shuffled control;* grey).

b) Area under the *repetition* bias curve (green) and *shuffled* bias curve (grey). c) Average response bias relative to the angular difference between the *cueing* orientation and the *repeated* orientation (*prospective* bias; blue) and between the *random* orientation and the *repeated* orientation in a subset of trials (*repetition* bias; green). d) Area under the *prospective* bias curve (blue) and *repetition* bias curve (green; calculated using a subset of trials; see **Methods**). e) Average response bias relative to the angular difference between the *repeated* orientation and subsequent *random* Gabors (*repetition retrospective* bias; yellow) and between adjacent *random* Gabors (*random retrospective* bias; pink). f) Area under the *repetition retrospective* bias curve (yellow) and the *random retrospective* bias curve (pink). Individual dots reflect the average AUC of each participant and error bars depict the SEM. Asterisks denote statistically significant differences following relevant statistical tests. Shaded areas reflect the SEM and the lines below the bias curves reflect orientation-bins that were significantly different between conditions following cluster-based permutation testing.

Subsequently, I investigated the bias exerted by the *repeated* orientation on *cueing* Gabors, which were predictive of the *repeated* orientation, and compared it to the *repetition* bias of the *repeated* Gabor on *random* grating reports (**Figure 2.2c,d**). Interestingly, neither cluster-based permutation testing nor a t-test of AUC revealed any differences between conditions (M_{rep}: 25.9, SD_{rep}: 131.3; M_{pros}: 16.95, SD_{pros}: 124.86; $t(48) = .58$, $p = .56$, $d = .08$). It was concluded that despite their predictive value, *cueing* Gabors were biased by the *repeated* orientation to the same extent as *random* Gabors.

Finally, a t-test comparing the AUC of *retrospective* biases following *repeated* vs *random* Gabors revealed that the *repetition retrospective* bias was stronger than the *random retrospective* bias (**Figure 2.2f**; M_{rep}: 81, SD_{rep}: 184.42; M_{rand}: 45.92, SD_{rand}: 143.68; $t(48) = 2.06$, $^*p = .04$, $d = .29$). In contrast, no significant clusters were identified using cluster-based permutation testing between the two bias curves (**Figure 2.2e**), suggesting that the *retrospective* bias exerted by *repeated* targets was only slightly stronger than that of *random* targets.

In summary, Experiment 1 showed that medium-term feature regularities, such as exposure to a repeating orientation, exerted a *repetition* bias on all other orientation reports. Interestingly, this bias did not differ for *cueing* Gabors which predicted the subsequent appearance of the *repeated* feature. Additionally, the *retrospective* bias exerted by the *repeated* feature seemed to be slightly stronger than the *retrospective* bias of other random features.

2.4 EXPERIMENT 2

The second experiment tested whether the effects described in Experiment 1 were contingent on explicit knowledge and predictability of the *repeated* orientation. As a secondary aim, Experiment 2 served to replicate and generalise the findings from Experiment 1 following minor modifications. Most importantly, the frequency of *repeated* Gabors increased from $1/6^{th}$ to $1/4^{th}$ of trials and the colour of the *repeated* Gabor changed between trials.

2.4.1 Methods

2.4.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R73580/RE001). The sample size for Experiment 2 was calculated based on Experiment 1. Fifty-four participants were recruited through the Prolific Academic platform (https://www.prolific.co). Pre-screening and payment of participants were the same as in Experiment 1. The same participant exclusion criteria as in Experiment 1 led to a final sample of 51 participants in subsequent analyses (mean age: 32.47; age range: 23-40; age SD: 4.3; 22 female and 29 male; 8 left-handed).

2.4.1.2 Experimental procedure and stimuli

Participants performed an orientation-reproduction task with the same basic stimulus features, timings, and orientation-report procedure as in Experiment 1. The experimental procedure differed only in the experimental details highlighted below (**Figure 2.3a**).

In Experiment 2, Gabor patches appeared in four colours instead of six (CIE, 2004; orange: #D55E00, blue: #0072B2, pink: #CC79A7, green: #009E73). For each participant, one *repeated* orientation was displayed more often than others ($1/4^{th}$ of trials). In all other trials, orientations were chosen randomly from a uniform distribution ranging from 1° to 180°.

Each participant completed 20 blocks containing 50 trials each. Half of the blocks corresponded to *explicit/predictable* blocks (hereafter, *predictable*). Conversely, the other half were *implicit/unpredictable* blocks (hereafter, *unpredictable*). In *predictable* blocks, one of the four colours corresponded to the *cueing* colour and trials in which the *cueing* colour was present were always followed by trials with the *repeated* orientation. Thus, in *predictable* blocks, the appearance of a Gabor with the *cueing* colour on one trial (N-1) was fully predictive of the appearance of a Gabor with the *repeated* orientation on the next trial (N). The contingency between the *cueing* colour and the *repeated* Gabor's orientation were explicitly disclosed to participants before each *predictable* block. In *unpredictable* blocks, the *repeated* orientation was also displayed in $1/4^{th}$ of the trials but, unlike *predictable* blocks, *repeated* Gabors were not preceded by *cueing* Gabors of a particular colour. Furthermore, the orientation of the *repeated* Gabor was not explicitly disclosed to participants.

In contrast to Experiment 1, *repeated* Gabors in both *predictable* and *unpredictable* blocks were not consistently coloured in Experiment 2. In *predictable* blocks, *repeated* Gabors were equiprobably coloured with one of the three non-cueing colours. In *unpredictable* blocks, they were equally likely to have any of the four background colours. This change from Experiment 1 to 2 aimed at isolating the effects of predictions about the *repeated* orientation from predictions about the colour and orientation of *repeated* Gabors.

The order of *predictable* and *unpredictable* blocks was randomised for each participant such that both types of blocks were intermixed. In each type of block, the orientation of the *repeated* Gabor was chosen randomly from one out of ten possible orientation bins spanning 180° (1-18°; 18-36°, 36-54°, 72-54°, 72-90°, 90-108°, 108-126°, 126-144°, 144-162°, 162-180°). The order of the orientation bins was randomised as in Experiment 1, such that both kinds of blocks displayed *repeated* Gabors chosen from each of the 10 orientation bins above. The orientation of the *repeated* Gabor was consistent for the duration of a block (medium-term feature regularity).

2.4.1.3 Data analysis and statistical testing

Data cleaning followed the same procedures as in Experiment 1. "Bad" trials were identified as in Experiment 1 separately for the two block types. An average of 2.06% (SD: 1.26%) trials were removed per participant.

Similar to Experiment 1, the differences in report error and RT between conditions were investigated using repeated-measures ANOVAs with condition (*repeated*, *cueing*, and *random*) and block type (*predictable* and *unpredictable)* as factors. In *unpredictable* blocks, *cueing* Gabors refer to those preceding the *repeated* orientation in the absence of any explicit contingency or predictive value.

Response-bias curves were calculated as detailed in Experiment 1 separately for *predictable* and *unpredictable* blocks. An average of 198.98 trials (SD: 60.48; *predictable*) and 285.04 trials (SD: 12.42; *unpredictable*) per participant were used for calculating both the *repetition* bias curve and the *shuffled control* condition. The *prospective* bias curve and its control *repetition* bias were both calculated with 69.22 trials (SD: 12.28; *predictable*) and 71.06 trials (SD: 4.61; *unpredictable*). An average of 70.18 trials (SD: 11.98; *predictable*) and 71.18 trials (SD: 4.22; *unpredictable*) were used to calculate both the *repetition retrospective* bias and the *random retrospective* bias. Statistical significance of the difference between conditions was probed using cluster-based permutation testing and AUC calculation followed by t-tests, as detailed above.

2.4.2 Results

2.4.2.1 General performance

First, participants' general performance was explored to test whether medium-term feature regularities influenced behaviour. A repeated-measures ANOVA of report error with condition (*repeated*, *cueing*, vs *random*) and block type (*predictable* vs *unpredictable*) as factors revealed a main effect of condition ($F(1,100) = 3.73$, $*p_{GG} = .049$, $\eta^2 = .006$; **Figure 2.3b**), no effect of block type ($F(1,50) = .91$, $p = .36$, $\eta^2 = .001$) and no interaction between condition and block type ($F(1,100) = 2.27$, $p = .12$, $\eta^2 = .003$). Post-hoc t-tests revealed that participants' errors were smaller when reporting *repeated* orientations (M_{rep}: 7.17°, SD_{rep}: 2.49°) than *random* orientations (M_{rand}: 7.37°, SD_{rand}: 2.45°; $t(50) = -2.06$, $*p = .04$, $d = .2$). Similarly, participants were more accurate at reporting *repeated* orientations than *cueing* Gabors (M_{cue}: 7.7°, SD_{cue}: 3.63°; $t(50) = -2.25$, $*p = .03$, $d = .22$). Thus, participants seemed to be more accurate at reporting *repeated* Gabors than *random* Gabors and *cueing* Gabors.

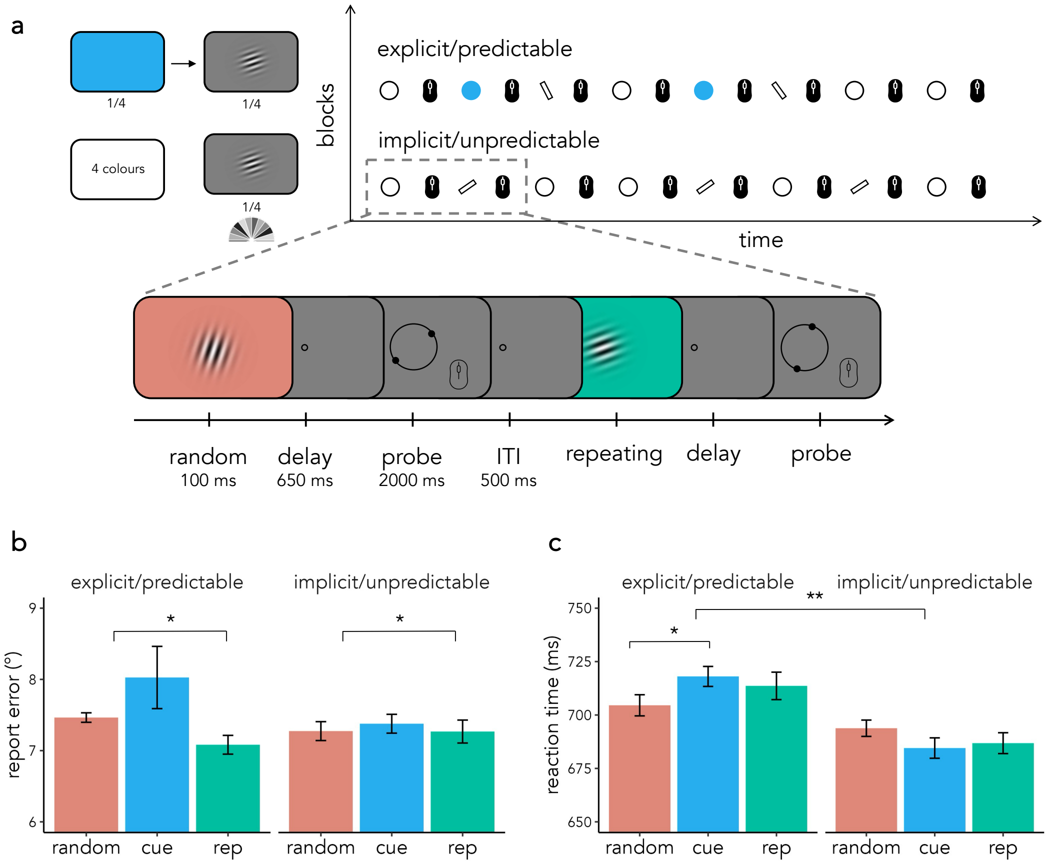


Figure 2.3. Experiment 2: task design and general performance. a) Trial schematic. In each trial, participants reported the orientation of a Gabor presented in one of four possible colours. In *predictable* blocks (10/20), one of the colours was randomly selected as the *cueing* colour. The colour of the Gabor in each trial was chosen randomly out of four possible colours and its orientation was chosen equiprobably from 1-180°. When the *cueing* colour was chosen in trial N-1, the following trial would display a Gabor with the *repeated* orientation (N). The *repeated* orientation was chosen from one out of 10 orientation bins spanning 180° and remained constant in each block. In *predictable* blocks, the orientation of the *repeated* Gabor and the predictive relation between the *cueing* colour and the *repeated* orientation was explicitly disclosed to participants at the beginning of the block. In *unpredictable* blocks (10/20), no *cueing* colour predicted the appearance of the *repeated* Gabor, and the *repeated* orientation was not explicitly disclosed to participants. b) Mean report error (°) to *random*, *cueing*, and *repeated* Gabors in *predictable* and *unpredictable* blocks. c) Mean reaction time (ms) to *random*, *cueing*, and *repeated* Gabors in *predictable* and *unpredictable* blocks. Error bars depict the SEM and asterisks denote statistically significant differences following relevant statistical tests.

Additionally, an ANOVA of RT with condition (*repeated*, *cueing*, vs *random*) and block type (*predictable* vs *unpredictable*) as factors revealed a main effect of block type

($F(1,50) = 12$, $^{**}p = .001$, $\eta^2 = .003$; **Figure 2.3c**), no main effect of condition ($F(1,100) = .14$, $p_{GG} = .85$, $\eta^2 < .000$) and an interaction between condition and block type ($F(1,100) = 6.15$, $^{**}p_{gg} = .004$, $\eta^2 = .0006$). Post-hoc t-tests showed that participants were slower at reporting *cueing* Gabors (*predictable* – M_{cue}: 718.05 ms, SD_{cue}: 197.58 ms; *unpredictable* – M_{cue}: 684.53 ms, SD_{cue}: 196.46 ms) than *random* Gabors (*predictable* – M_{rand}: 704.54 ms, SD_{rand}: 199.64 ms; *unpredictable* – M_{rand}: 693.81 ms, SD_{rand}: 194.94 ms) only in *predictable* blocks ($t(50) = 2.77$, $^{*}p = .02$, $d = .39$) and not *unpredictable* blocks ($t(50) = -2.5$, $p = .16$, $d = .35$). No differences were found for *repeated* vs *random* Gabors (*predictable* – M_{rep}: 713.6 ms, SD_{rep}: 209.6 ms; $t(50) = 1.39$, $p = .17$, $d = .19$; *unpredictable* – M_{rep}: 686.81 ms, SD_{rep}: 187.83 ms; $t(50) = -1.81$, $p = .32$, $d = .25$).

Participants were generally more accurate at reporting *repeated* orientations. Moreover, explicit knowledge and predictability of the *repeated* Gabor led to a general slowing of responses to *cueing* Gabors. Additionally, participants were slower in *predictable* than in *unpredictable* blocks, presumably reflective of the use of different behavioural strategies. Thus, the blocked manipulation of the explicitness and predictability of the *repeated* orientation successfully influenced participants' behaviour as measured with RT.

2.4.2.2 Perceptual biases

The next step was to investigate whether and how exposure to the *repeated* orientation biased the perception of *random* Gabors. Cluster-based permutation testing revealed the presence of a *repetition* bias in both block types (**Figure 2.4a**; left to right; *predictable – cluster* (7 to 34): $^{**}p = .001$; *unpredictable – cluster 1 (-44 to -5)*: $^{***}p < .001$; *cluster 2 (10 to 34)*: $^{**}p = .001$). An ANOVA of AUC with condition (*repeated*, *cueing,* vs *random*) and block type (*predictable* vs *unpredictable*) as factors revealed a main effect of condition, thus further confirming the presence of a *repetition* bias (**Figure 4b**; $F(1,50) = 15.46$, $^{***}p < .001$, $\eta^2 = .07$). Strikingly, there was no effect of block type (*predictable* vs *unpredictable*) on AUC and no interaction between the factors ($F(1,50) = .29$, $p = .59$, $\eta^2 = .001$; $F(1,50) = .28$, $p = .59$, $\eta^2 = .002$). Together, these results suggested that participants systematically reported *random* Gabors as more dissimilar to the *repeated* orientation, regardless of whether the medium-term feature regularity was explicit and predictable (**Figure 2.4a,b**).

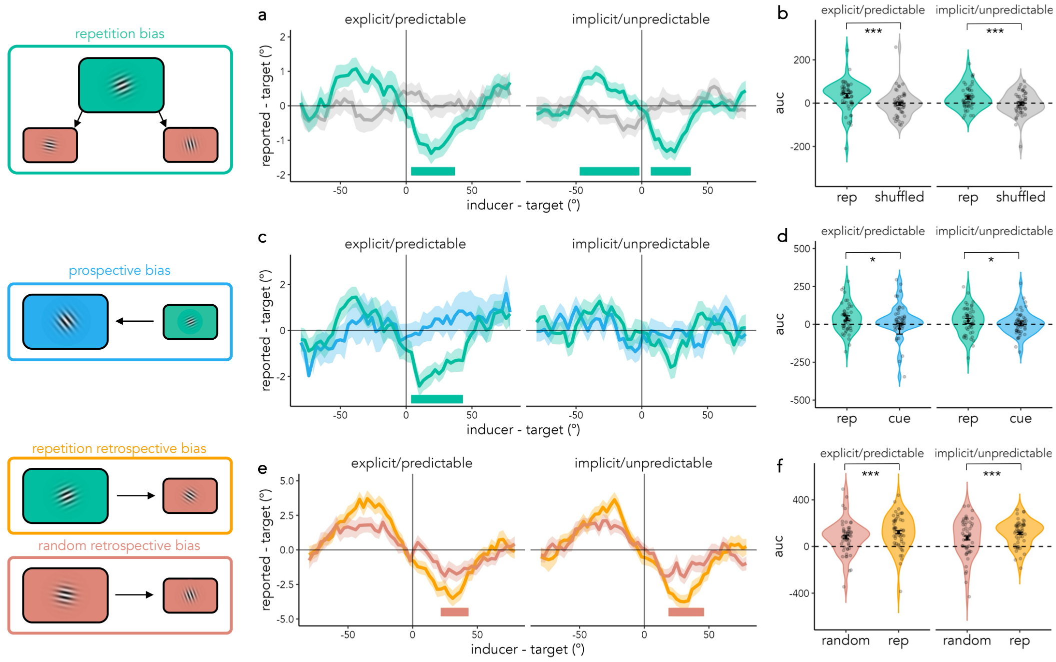


Figure 2.4. Experiment 2: repetition bias, prospective bias, and retrospective biases. a) Average response bias relative to the angular difference between *random* Gabors and the *repeated* orientation (*repetition* bias; green) and between *random* Gabors and the *shuffled repeated* orientation (*shuffled control;* grey) in *predictable* and *unpredictable* blocks. b) Area under the *repetition* bias curve (green) and *shuffled* bias curve (grey) in *predictable* and *unpredictable* blocks. c) Average response bias relative to the angular difference between the *cueing* orientation and the *repeated* orientation (*prospective* bias; blue) and between the *random* orientation and the *repeated* orientation in a subset of trials (*repetition* bias; green) in *predictable* and *unpredictable* blocks. d) Area under the *prospective* bias curve (blue) and *repetition* bias curve (green; calculated using a subset of trials; see **Methods**) in *predictable* and *unpredictable* blocks. e) Average response bias relative to the angular difference between the *repeated* orientation and subsequent *random* Gabors (*repetition retrospective* bias; yellow) and between adjacent *random* Gabors (*random retrospective* bias*;* pink) in *predictable* and *unpredictable* blocks. f) Area under the *repetition retrospective* bias curve (yellow) and the *random retrospective* bias curve (pink) in *predictable* and *unpredictable* blocks. Individual dots reflect the average AUC of each participant and error bars depict the SEM. Asterisks denote statistically significant differences following relevant statistical tests. Shaded areas reflect the SEM and the lines below the bias curves reflect orientation-bins that were significantly different between conditions following cluster-permutation testing.

Subsequently, I compared the *prospective* bias exerted by the *repeated* orientation on *cueing* Gabors with the *repetition* bias of the *repeated* Gabor on *random* grating reports (**Figure 2.4c, d**). Interestingly, cluster-based permutation testing revealed a significant cluster between the *prospective* and *repetition* bias curves in *predictable* blocks only (**Figure 2.4c**; *cluster* (7 to 40): **p = .001). Additionally, an ANOVA of AUC with condition (*repeated*, *cueing,* vs *random*) and block type (*predictable* vs *unpredictable*) as factors revealed a main effect of condition ($F(1,46) = 5.17$, *$p = .03$, $\eta^2 = .024$), no main effect of block type ($F(1,46) = .26$, $p = .61$, $\eta^2 = .001$) and no interaction between the factors ($F(1,46) = 1.58$, $p = .22$, $\eta^2 = .007$). Together, these results provided preliminary evidence for a small diminishment of the *prospective* bias with respect to the *repetition* bias, especially in *predictable* blocks. This suggested that participants were slightly less biased away from the *repeated* orientation during *cueing* trials which were predictive of the upcoming appearance of a *repeated* orientation.

Furthermore, the *retrospective* bias induced by the *repeated* orientation was stronger than that induced by any other *random* Gabor in both block types (**Figure 2.4e**; *predictable – cluster* (25 to 40): *p = .03; *unpredictable – cluster (22 to 43*): **p = .007). Additionally, an ANOVA of AUC with condition (*repeated*, *cueing,* vs *random*) and block type (*predictable* vs *unpredictable*) as factors revealed a main effect of condition ($F(1,46) = 14.27$, ***$p < .001$, $\eta^2 = .038$; **Figure 2.4f**), no main effect of block type ($F(1,46) = .16$, $p = .69$, $\eta^2 < .000$) and no interaction between the factors ($F(1,46) = .27$, $p = .6$, $\eta^2 < .000$). Together, these findings suggested that the *repeated* orientation exerted a larger perceptual bias on subsequent *random* Gabors than any *random* orientation.

Experiment 2 replicated most of the findings from Experiment 1, showing that a frequently displayed stimulus orientation within a block (medium-term feature regularity) exerts a general repulsive bias on other orientation reports (*repetition* bias). Additionally, it confirmed the trend observed in Experiment 1 that the *retrospective* bias of the *repeated* orientation was stronger than that of other *random* orientations. Interestingly, in contrast to Experiment 1, Experiment 2 revealed that the bias exerted by the *repeated* feature on predictive, *cueing* Gabors (*prospective* bias) seemed to be slightly smaller than the effect on *random* orientations (*repetition* bias). This effect seemed to be particularly prominent in blocks in which the *cueing* colour was explicitly predictive of the *repeated* orientation. Nevertheless, it was a small effect.

2.5 EXPERIMENT 3

In addition to replicating the findings from Experiments 1 and 2, the aim of Experiment 3 was to elucidate whether the *repetition* biases related to the medium-term feature regularity were dependent on having to respond to the *repeated* orientation.

2.5.1 Methods

2.5.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R73580/RE001). The sample size for Experiment 3 was calculated based on Experiments 1 and 2. Fifty-five participants were recruited through the Prolific Academic platform (https://www.prolific.co). Pre-screening and payment of participants were the same as in Experiments 1 and 2. The same participant exclusion criteria as in previous experiments resulted in excluding data from 7 participants, leaving a final sample size of 48 in subsequent analyses (mean age: 33.67; age range: 23-40; age SD: 4.9; 11 female and 37 male; 6 left-handed).

2.5.1.2 Experimental procedure and stimuli

Participants performed an orientation report task with the same basic stimulus features, timings, and orientation report procedure as in Experiments 1 and 2. The experimental details differed as explained below (**Figure 2.5a**).

In Experiment 3, a *repeated* orientation was shown more often than any other orientation (1/4th of trials). As in the *unpredictable* blocks of Experiment 2, the *repeated* orientation was never predictable, and its orientation was not disclosed to participants. Importantly, in Experiment 3, participants only reproduced the orientation of 50% of the displayed Gabors. The requirement to respond was randomly determined on every trial. The appearance of a dial after the stimulus determined whether participants should respond to the previously presented Gabor. If a dial was displayed, participants had to report the orientation of the stimulus. If the fixation circle remained on the screen and the dial did not appear, participants did not respond. In trials that did not require an orientation report, the fixation circle remained on the screen *in lieu* of the dial, thus matching the duration of both trial types.

In Experiment 3, participants completed 20 blocks composed of 50 trials each. Half of the blocks corresponded to *repeated Gabor response* blocks (hereafter, *response* blocks) and the other half were *repeated Gabor no response* blocks (hereafter, *no response* blocks). In *response* blocks, *random* and *repeated* Gabors had the same probability (50%) of requiring a response. Alternatively, in *no response* blocks, *repeated* Gabors never required an orientation report. The order of block types was randomised and the orientation of the *repeated* Gabor in each block was chosen as detailed in Experiment 2, such that blocks of both kinds displayed *repeated* orientations from each the 10 non-repeated orientation bins.

2.5.1.3 Data analysis and statistical testing

Data cleaning followed the same procedure as in Experiment 2. "Bad" trials were identified separately for each block type, and an average of 1% (SD: 0.51%) of trials were removed per participant.

Due to an absence of responses to *repeated* Gabors in *no response* blocks, the *condition* variable had two levels corresponding to *repeated* and *random* orientations in *response* blocks only. Additionally, there were no *cueing* Gabors in Experiment 3. Therefore, the dependent variables were compared between conditions using paired-sample t-tests.

Response-bias curve calculation was performed as detailed in Experiments 1 and 2 separately for *response* and *no response* blocks. An average of 115.1 trials (SD: 7.28; *response*) and 147.27 trials (SD: 10.82; *no response*) per participant were used for the calculation of both the *repetition* bias curve and the *shuffled control* condition. An average of 60.17 trials (SD: 6.12; *response*) and 76.23 trials (SD: 6.5; *no response*) were used to calculate both the *repetition retrospective* bias the *random retrospective* bias. Statistical significance was tested using cluster-based permutation testing and AUC calculation followed by t-tests, as detailed above.

2.5.2 Results

2.5.2.1 General performance

A paired-samples t-test of *repeated* vs *random* Gabors in *response* blocks revealed no significant differences between conditions in report error (**Figure 2.5b**; M_{rep}: 8.06°, SD_{rep}: 4.83°, M_{rand}: 8.32°, SD_{rand}: 5.59°, $t(46) = -1.37$, $p = .18$, $d = .2$). Nevertheless, participants were consistently faster at responding to *repeated* as opposed to *random* Gabors (**Figure 2.5c**; M_{rep}: 1111.37 ms, SD_{rep}: 178.28 ms, M_{rand}: 1138.42 ms, SD_{rand}: 182.5 ms, $t(46) = -4.63$, $^{***}p < .001$, $d = .67$). Therefore, despite its implicit and unpredictable nature, the repetition of an orientation seemed to fasten participants' responses to that feature.

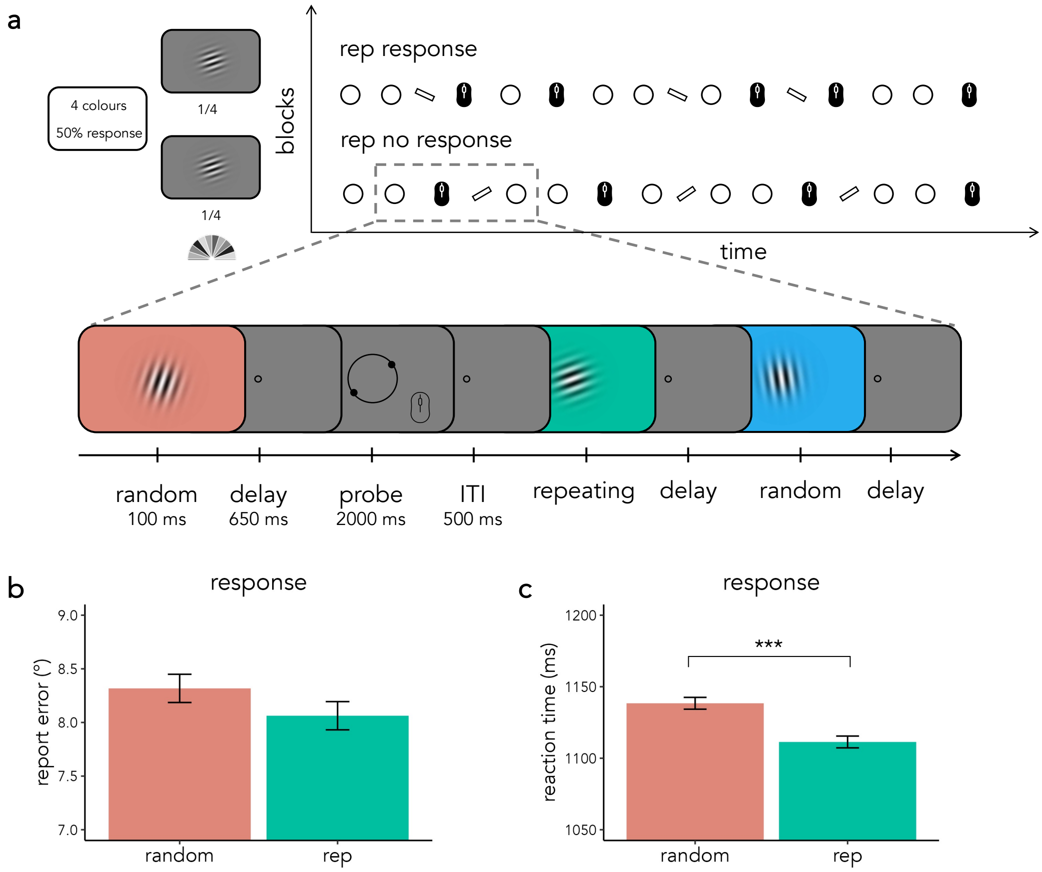


Figure 2.5. Experiment 3: task design and general performance. a) Trial schematic. In each trial, participants reported the orientation of a Gabor patch coloured in one out of four possible colours. A *repeated* orientation was shown in 1/4th of trials of a block. The *repeated* orientation was unpredictable, and it was not explicitly disclosed to participant. Participants only reported the orientation of Gabors in half of the trials and had to hold off their responses in the other half. In *response* blocks (10/20), participants were equally likely to report the orientation of *random* and *repeated* Gabors. In *no response* blocks (10/20), participants never reported the orientation of *repeated* Gabors despite being exposed to them in 1/4th of the trials. b) Mean report error (°) to *random* and *repeated* Gabors in *response* blocks. c) Mean reaction time (ms) to *random* and *repeated* Gabors in *response* blocks. Error bars depict the SEM and asterisks denote statistically significant differences following relevant statistical tests.

2.5.2.2 Perceptual biases

Consistent with the findings reported in Experiments 1 and 2, cluster-based permutation analyses of response-bias curves showed that participants were systematically biased by the *repeated* orientation in their orientation reports of *random*

Gabors (**Figure 2.6a**; left to right; *response – cluster 1* (-59 to -44): *$p = .03$, *cluster 2* (16 to 43): **$p = .001$; *no response – cluster 1 (-47 to -20)*: ***$p < .001$; *cluster 2 (28 to 37)*: *$p = .04$). This was confirmed by a 2x2 ANOVA of AUC with condition (*repeated* vs *random*) and block type (*response* vs *no response*) as factors, which revealed a main effect of condition ($F(1,47) = 60.64$, ***$p < .001$, $\eta^2 = .19$; **Figure 2.6b**). Interestingly, block type did not influence the *repetition* bias ($F(1,47) = .18$, $p = .67$, $\eta^2 = .002$) and the factors did not interact ($F(1,47) = .25$, $p = .62$, $\eta^2 = .001$). Together, the complementary analyses revealed that participants reported *random* Gabors as more dissimilar to the *repeated* orientation regardless of whether *repeated* Gabors had to be reported. Therefore, it was concluded that exposure to the medium-term statistic (i.e., *repeated* feature) was sufficient for the *repetition* bias to emerge and that engaging an active motor process by reporting its orientation was not necessary.

The *retrospective* bias induced by the *repeated* orientation on a subsequent *random* orientation report was stronger than the *retrospective* bias between *random* targets in *response* blocks (**Figure 2.6c**; *cluster* (-35 to -17): ***$p < .001$). No clusters were found in *no response* blocks. This pattern of findings was similar in a 2x2 ANOVA of AUC with condition (*repeated* vs *random*) and block type (*response* vs *no response*) as factors which revealed a main effect of condition ($F(1,46) = 8.29$, **$p = .006$, $\eta^2 = .03$; **Figure 2.6d**), no main effect of block type ($F(1,46) = .0001$, $p = .99$, $\eta^2 = .0008$) and no interaction between the factors ($F(1,46) = .17$, $p = .68$, $\eta^2 < .000$). These results suggested that the *retrospective* bias of the *repeated* feature was stronger than the *retrospective* bias between *random* features.

Experiment 3 concluded that exposure to a *repeated* feature was sufficient for the *repetition* bias to emerge. Moreover, the *retrospective* bias exerted by the *repeated* orientation was enhanced compared to *random* Gabors in both *response* and *no response* blocks.

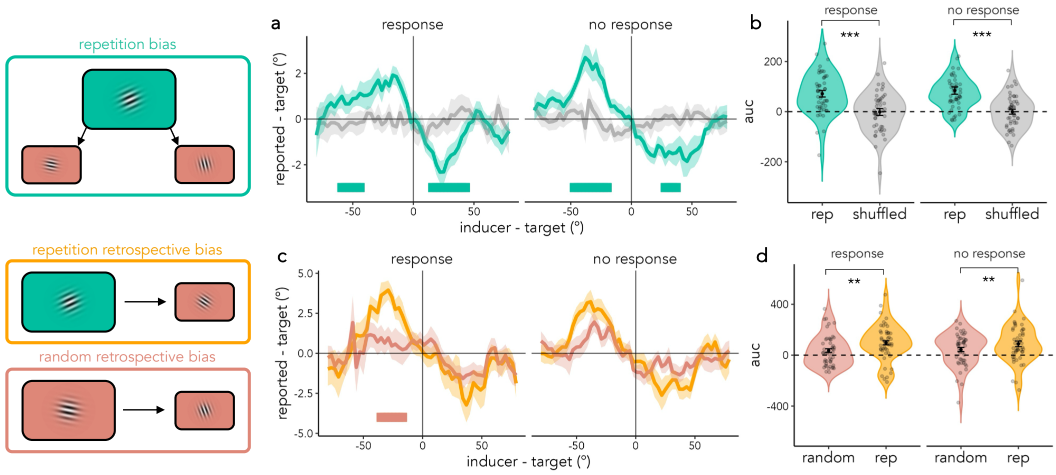


Figure 2.6. Experiment 3: repetition bias and retrospective bias. a) Average response bias relative to the angular difference between *random* Gabors and the *repeated* orientation (*repetition* bias; green) and between *random* Gabors and the *shuffled repeated* orientation (*shuffled* bias; grey) in *response* and *no response* blocks. b) Area under the *repetition* bias curve (green) and *shuffled* bias curve (grey) in *response* and *no response* blocks. c) Average response bias relative to the angular difference between the *repeated* orientation and subsequent *random* Gabors (*repetition retrospective* bias; yellow) and between adjacent *random* Gabors (*random retrospective* bias; pink) in *response* and *no response* blocks. d) Area under the *repetition retrospective* bias curve (yellow) and the *random retrospective* bias curve (pink) in *response* and *no response* blocks. Individual dots reflect the average AUC of each participant and error bars depict the SEM. Asterisks denote statistically significant differences following relevant statistical tests. Shaded areas reflect the SEM and the lines below the bias curves reflect orientation-bins that were significantly different between conditions following cluster-based permutation testing.

2.6 DISCUSSION

Across three orientation-reproduction experiments, the present study investigated the effects of medium-term feature regularities on perception. Medium-term feature regularities were manipulated by repeating one orientation more frequently among other intervening *random* orientations. The consequences of exposure to this feature regularity on perception were estimated by calculating perceptual biases to the *repeated* feature. Additionally, this study investigated the effects of explicit predictability and the requirement to respond to the *repeated* feature on perceptual biases.

The feature regularity affected participants' general performance across all experiments. When it was explicit and predictable, the *repeated* orientation was reported more accurately but more slowly than *random* orientations (Experiments 1). Alternatively, when it was unpredictable and implicit, participants were faster at reporting the *repeated* orientation than *random* orientations but equally as accurate (Experiment 3). A limitation of Experiment 3 is that, despite a lack of responses to *repeated* features in *no response* blocks, participants could have prepared their responses. While this is unlikely given the higher RTs in Experiment 3 as opposed to 1 and 2, the present design cannot completely rule out this possibility. Uncertainty about the required response could be introduced to address this concern directly.

Exposure to a *repeated* orientation resulted in a tendency to report other orientations as more dissimilar to the former (*repetition* bias). This was replicated across three experiments that differed in experimental parameters such as the proportion of *repeated* orientations ($1/6^{th}$ vs $1/4^{th}$ of trials in a block) and the predictability of the *repeated* Gabor's colour (*predictable* vs *unpredictable*). Interestingly, the *repeated* orientation exerted a biasing effect regardless of whether it was explicitly instructed to participants and despite its predictability from the previous trial (Experiments 1 and 2). Additionally, exposure to the *repeated* orientation without having to respond to it was sufficient for the *repetition* bias to emerge (Experiment 3). Therefore, the main conclusion of this study is that exposure to medium-term feature regularities (i.e., repeated exposure to a feature during a block) results in systematic biases in perception despite predictability and relevance. This is in line with other studies which have also found perceptual biases following exposure to two frequent motion directions (Chalk et al., 2010; see also Gekas et al., 2013, 2015; Sotiropoulos et al., 2011), cued orientations (Kok et al., 2013), and colour (Scotti et al., 2021).

An additional question addressed by the present study was whether the *repetition* bias changed around the predicted time of *repeated* feature appearance. To investigate this, I calculated the bias exerted by the *repeated* orientation on the immediately preceding *cueing* Gabors (*prospective* bias) and found mixed effects. In Experiment 1, the *prospective* bias was no different to the *repetition* bias. Alternatively, Experiment 2 revealed that *cueing* Gabors were slightly less biased by the *repeated* orientation than *random* ones, particularly when the contingency was explicit and predictable. The observed disparity could result from design-related differences such as the higher frequency of *repeated* orientations in Experiment 2 vs 1 (1/4th vs 1/6th) or the predictability of the background colour of *repeated* Gabors in Experiment 1 but not 2. Nevertheless, the magnitude of the *repetition* bias in Experiments 1 and 2 was similar which argues against this possibility. Moreover, the difference between the *prospective* and *repetition* bias in Experiment 2 was calculated using a smaller number of trials and it was a small effect.

The lack of a consistent difference between the perceptual biases exerted by the *repeated* feature on immediately preceding (predictive) *cueing* orientations vs *random* orientations is somewhat puzzling. It is in contrast with studies which have found a modulation of brain activity patterns specific to expected features (Aitken et al., 2020; Demarchi et al., 2019; Kok et al., 2012, 2013). Nevertheless, most of these studies report activity changes soon before the onset of the expected feature (~40 ms; Kok et al., 2017) while, in this study, the *prospective* bias was calculated ~2 s before the appearance of expected feature, in the previous trial. Therefore, perceptual biases to the upcoming orientation may emerge closer to the expected time of *repeated* orientation appearance. Alternatively, the changes in underlying brain activity patterns could be independent from perceptual biases, which could account for the inconsistency of the effects in the present study.

Most of the presented results show that the *retrospective* bias exerted by the *repeated* orientation was stronger than the *retrospective* bias of *random* orientations. This suggests that *retrospective* and *repetition* biases modulate perception concurrently and, more broadly, that multiple types of biases operate on perception at the same time. This result is consistent with studies that have found interactions between biases to feature regularities such as the central tendency effect and serial biases (Bae, 2024; Pinchuk-Yacobi et al., 2016). At the extreme, some studies have claimed that both kinds of biases reflect the same process (Akrami et al., 2018; Boboeva et al., 2023; Hahn & Wei, 2024; Sailor & Antoine, 2005; Tong & Dubé, 2022), while others have argued for their independent nature (Cicchini et al., 2022, 2024; Lieder et al., 2019; Pascucci et al., 2023; Saarela et al., 2023).

Of note, the difference between the *repetition retrospective* bias and *random retrospective* bias is not consistent across all experiments in the present study. These small disparities could be the product of differences in the proportion of *repeated* orientations between Experiments 1 and 2 and of the requirement to respond to *repeated* orientations in Experiment 3. Alternatively, they could be the product of poor online data quality (Sauter et al., 2020). Nevertheless, all experiments show a trend towards statistical significance in the difference between *repetition retrospective* and *random retrospective* biases, suggesting that this is probably a small but consistent effect. There may be interesting functional differences between *repetition* and *retrospective* biases which could be further explored in the future. Interestingly, the magnitude of the *repetition retrospective* bias does not seem to reflect the summation of the *random retrospective* bias and the *repetition* bias, hinting at a non-additive relation between both. Alternatively, this could be the product of ceiling effects whereby the magnitude of perceptual biases tends to remain relatively small.

A few recent studies have demonstrated that feature distribution manipulations modulate serial biases. For example, uniform and Gaussian feature distributions result in serial effects in opposite directions (Blondé et al., 2023; see also Gekas et al., 2019; Scotti et al., 2021; Taubert et al., 2016). Additionally, computational models better describe the behavioural effects of serial dependence when they include parameters describing not only the immediate past, but also the distribution of longer-term statistics in the environment (Chopin & Mamassian, 2012; Gekas et al., 2019; Glasauer & Shi, 2022; Kalm & Norris, 2018; van Bergen & Jehee, 2019). Together, these findings speak to interesting relations between serial biases and perceptual biases formed from exposure to regularities over time which merit further investigation.

Despite an effort to reduce the lingering effects of retrospective biases on the *repetition* bias in this study (see **Methods**), it could theoretically reflect the summation of local retrospective biases. In fact, the serial bias of a feature in trial N is observed up to 3-5 trials later (for meta-analysis see Manassi et al., 2023). Nevertheless, the amplified *retrospective* bias of the *repeated* feature preliminary argues against this possibility.

The present study reports perceptual biases away from both the repeated feature (*repetition* bias and *prospective* bias) and the feature in the previous trial (*retrospective* bias). In contrast, perceptual biases have been mostly reported towards the immediately preceding feature (serial dependence; Cicchini et al., 2018; Czoschke et al., 2019; Fischer et al., 2020; Fischer & Whitney, 2014; Manassi & Whitney, 2022) and towards repeated features (Chalk et al., 2010; Gekas et al., 2013, 2015; Kok et al., 2013; Sotiropoulos et al., 2011). However, some studies have found negative serial biases (Bliss et al., 2017; Blondé et al., 2023; Gekas et al., 2019) which co-exist with positive ones (Fritsche et al., 2020; Gekas et al., 2019; Moon & Kwon, 2022). Similarly, exposure to medium-term regularities can also result in repulsive biases (e.g., Scotti et al., 2021). The significance of the directionality of biases remains debated, but recent proposals have suggested that they reflect the same underlying phenomenon (Hahn & Wei, 2024; Wei & Stocker, 2015).

The negative direction of the reported biases could reflect the choice of stimulus parameters. Specifically, the following features of the present task have previously been shown to result in negative rather than positive biases: 1) high certainty and visibility of targets (high contrast and no masking; for meta-analysis see Manassi et al., 2023), 2) a short delay between target appearance and response (Bliss et al., 2017), and 3) task designs which do not require responses to every target (Experiment 3; i.e., Blondé et al., 2023; Gekas et al., 2019). Using terms borrowed from Bayesian probability theory, in this task, sensory certainty and expectation reliability were both high. The chosen stimuli were highly visible and distinguishable, as evidenced by the high accuracy of participants' orientation reports. Additionally, the explicit disclosure of the *repeated* feature and its predictability following *cueing* Gabors resulted in the formation of strong and reliable predictions about the *repeated* feature. Moreover, *repeated* orientations were also temporally predictable, as the ISIs and ITIs were constant across trials. The reliance on the expectancy of *repeated* orientations is supported by the differential behavioural patterns seen for both *repeated* and *cueing* Gabor reports (Experiment 1) and by participants' accurate responses when asked about the *cueing-repeated* Gabor contingencies.

Under the Bayesian framework, the reliability of sensory inputs and of expectations (priors) seem to be two key determinants of the perceptual and behavioural consequences of expectations (de Lange et al., 2018). Consistently, perceptual biases are particularly prominent when sensory evidence is low (e.g., Chalk et al., 2010). In the present study, the reliability of the sensory evidence was high and, therefore, participants need not rely on expectations. Additionally, the *repeated* features were highly predictable, and it is known that some amount of variability in stimulus features (e.g., Brady, 1998; Szpiro et al., 2014) and timings (Shdeour et al., 2024) benefits learning. Thus, the high reliability of sensory signals and expectations in this task may explain the inconsistent differences between the bias exerted by the *repeated* feature on *cueing* (predictive) Gabors vs *random* Gabors. Speculatively, increasing sensory uncertainty in this task may result in positive perceptual biases and enhancing expectation uncertainty may lead to differences between the *prospective* bias and the general *repetition* bias.

The mechanisms whereby medium-term feature regularities and other expectations may have resulted in perceptual biases in this task remain elusive. Several studies have found a reduction in activity in related sensory areas, while the underlying activity patterns have been found to reflect the expected feature (Aitken et al., 2020; Demarchi et al., 2019; Kok et al., 2012, 2013, 2017; see also Chelazzi et al., 1993; Luck et al., 1997; Martinez-Trujillo & Treue, 2004; Serences et al., 2009; Stokes et al., 2009). Relatedly, exposure to repeated stimuli is known to suppress neural activity (repetition suppression; e.g., Summerfield et al., 2008). Additionally, visual adaptation is known to change the tuning curves of V1 neurons (Clifford, 2002; Clifford et al., 2007; Kohn, 2007; Thompson & Burr, 2009; Weber et al., 2019; Webster, 2015). Recently, Fritsche and colleagues (2022) showed that a briefly presented grating can induce feature-specific changes in the properties of V1 neurons which persist for dozens of seconds in the midst of intervening stimuli. In the present study, one, all, or neither of these neural mechanisms may be at play. Future efforts should be devoted to investigating the neural mechanisms whereby statistics across several timescales modulate perceptual systems.

Studies investigating the neural and behavioural consequences of expectations have done so in at least two ways. In some studies, feature regularities are displayed over time, and they are thought to be learned implicitly giving rise to expectations which, subsequently, bias perception (e.g., Chalk et al., 2010). Alternatively, expectations have been manipulated by explicitly instructing participants to expect specific stimuli (e.g., Kok et al., 2012). Interestingly, while the main behavioural consequence of the latter is to improve task-performance, the former additionally results in perceptual biases (de Lange et al., 2018). In the present study, the *repeated* feature was displayed more frequently (exposure to feature regularities over time), and it was specifically expected after *cueing* Gabors (short-term predictive relations between events). While the present study cannot separate the behavioural consequences and perceptual biases that are due to each kind of expectation, future studies could build on the present design to disentangle the effects of these two sources of expectations on perception.

Additionally, there is a growing interest in trying to disentangle the effects of relevance and expectation on perception and attention (for review see Rungratsameetaweemana & Serences, 2019; Summerfield & de Lange, 2014). In most studies, attention is guided to expected attributes that are also relevant to the task (e.g., Posner, 1980), but expectation and relevance seem to have differing effects on perception and attention (Bang & Rahnev, 2017; Jiang et al., 2013; Rungratsameetaweemana et al., 2018; Wyart et al., 2012). The current study manipulates behavioural relevance of the *repeated* (expected) feature by cueing its appearance (Experiments 1 and 2) and by changing the requirement to respond to it (Experiment 3). Future studies could build on the present design to disambiguate between the effects of relevance and expectation on perception.

The current study presents a simple experimental design in which shorter- and longer-term task-statistics can be carefully manipulated and their joint effects on perceptual biases can be quantified. This design is additionally amenable to the investigation of interactions between biases emerging from shorter- and longer-term statistics and can be used to experimentally test the predictions made by computational models (e.g., Hahn & Wei, 2024; Tong & Dubé, 2022). The simplicity of the stimulus features and responses in this design makes it easily compatible with more complex manipulations of the statistical structure of the environment (Fiser & Lengyel, 2022; Schapiro & Turk-Browne, 2015). Additionally, this task is easily applicable to other stimulus features and sensory domains.

Overall, the present findings add to a growing body of theoretical (Chopin & Mamassian, 2012; Glasauer & Shi, 2022; Hahn & Wei, 2024; Kalm & Norris, 2018; Tong & Dubé, 2022; van Bergen & Jehee, 2019) and empirical (Akrami et al., 2018; Bae, 2024; Blondé et al., 2023; Boboeva et al., 2023; Gekas et al., 2019; Pinchuk-Yacobi et al., 2016; Scotti et al., 2021; Taubert et al., 2016) work reporting that feature regularities across several timescales concurrently shape perception. Nevertheless, several questions remain open about how feature regularities shape perception across different timescales. Do they act at the same processing stage? If not, when do they become integrated? Are they causally responsible for the observed behavioural benefits? Are they intrinsically linked to expectations? What is(are) their functional role(s)? These and other questions could be addressed by future research efforts.

3 FLEXIBLE USE OF TEMPORAL EXPECTATIONS IN EXTERNAL ATTENTION

3.1 ABSTRACT

The temporal regularities in our environments support the proactive dynamic anticipation of relevant events. One important outstanding question is whether temporal predictions about visual and auditory events must be linked to predictions about spatial locations or motor plans to facilitate behaviour. To test this, I developed a task for manipulating temporal expectations and task relevance of visual (Experiments 1 and 2) and auditory (Experiment 3) stimuli appearing within rapidly presented streams, while stimulus location and responding hand remained uncertain. Different target stimuli appeared in one of two concurrent (left and right) streams with distinct temporal probability structures. Targets were defined by colour (Experiments 1 and 2) or pitch (Experiment 3) on a trial-by-trial basis and appeared equiprobably in either stream, requiring a localisation response. Across three experiments, participants were faster and, in some cases, more accurate at detecting temporally predictable targets compared to temporally unpredictable targets. It is concluded that temporal expectations learned incidentally from temporal regularities can be called upon flexibly in a goal-driven manner to guide external attention. Moreover, visual and auditory

temporal attention are shown to facilitate performance in the absence of concomitant spatial or motor expectations in dynamically unfolding contexts.

3.2 Introduction

Consistent temporal structuring of events is prevalent in daily experience, ranging from regular isochronous rhythms (e.g., footsteps) to more complex sequences (e.g., music). These temporal regularities embedded in our environments give rise to expectations about *when* events are likely to occur, which, in turn, proactively guide selective anticipatory attention (for reviews see Correa, 2010; Nobre & Rohenkohl, 2014; Nobre & van Ede, 2018, 2023; Vangkilde et al., 2013). In the present study, I consider how two fundamental factors guide the orienting of attention to the timing of visual and auditory stimuli – expectations and task goals.

Temporal expectation has been suggested to exert its effects by latching onto other relevant anticipated stimulus attributes and modulating them at predictable times (Nobre & Rohenkohl, 2014). Joint expectations about the location and timing of a stimulus (spatiotemporal expectations) have consistently been reported to facilitate performance (e.g., Boettcher et al., 2022; Doherty et al., 2005; Lange & Röder, 2010; MacKay & Juola, 2007; Rieth & Huber, 2013; Rolke et al., 2016; Seibold et al., 2020; Weinbach et al., 2015). Furthermore, temporal expectation modulates the firing rates of neurons coding the locations of anticipated task-relevant stimuli (e.g., Ghose & Maunsell, 2002; Janssen & Shadlen, 2005). At the extreme, some studies have reported that temporal expectation in the absence of spatial certainty fails to facilitate behaviour, instead acting only by amplifying the effects of spatial expectations (e.g., Doherty et al., 2005; O'Reilly et al., 2008; Rohenkohl et al., 2014; Seibold et al., 2020).

In parallel, temporal expectation has been proposed to act by modulating preparatory motor activity at specific times, thus speeding response times (Boettcher et al., 2021; Heideman, et al., 2018; Miniussi et al., 1999; Thomaschke & Dreisbach, 2013; Trillenberg et al., 2000; van Ede et al., 2020; van Elswijk et al., 2007). However, it is debated whether temporal expectation modulates specific motor programs, or instead acts by exerting a more general influence on motor processes (Cotti et al., 2011; Kornysheva et al., 2013; Shin & Ivry, 2002). Indeed, in most studies investigating visual temporal expectation, the locations of expected targets and/or the required responses are kept constant or predictable. Consequently, it is currently unknown whether allocating attention to points in time based on temporal expectation can facilitate behaviour in the absence of spatial or action-related certainty.

The effects of temporal attention on behaviour have been studied using different experimental approaches. Tasks using predictive or instructive temporal cues (Coull & Nobre, 1998; Denison et al., 2017; Griffin et al., 2002; Nobre, 2001) have grounded most of the research on temporal attention. Like their spatial counterpart, temporal cueing tasks use cues to indicate when a stimulus will likely be displayed (e.g., Coull & Nobre, 1998) or which stimulus is goal-relevant based on its timing (Denison et al., 2017, 2021; Fernández et al., 2019; Griffin et al., 2002). In turn, the predictive or instructive cues deploy endogenous attention to moments in time (for reviews see Correa, 2010; Nobre, 2010). In contrast, in most everyday situations, attention is typically guided by predictions formed through the incidental learning of regularities in the environment. In the case of spatial attention, repeated contextual spatial configurations can guide attention to specific locations (Chun & Jiang, 1998). Similarly, targets preceded by repeating temporal patterns are more readily attended and better detected (Olson & Chun, 2001).

Task designs using informative endogenous cues vs incidental contextual learning capture complementary aspects of how temporal expectations are formed and utilised in real-world behaviour (Tal-Perry & Yuval-Greenberg, 2022). On the one hand, contextual cueing tasks simulate real-world scenarios by emphasising the incidental learning of temporal regularities that can guide expectation-based attention (Beck et al., 2014; Boettcher et al., 2022; Heideman et al., 2018; O'Reilly et al., 2008; Rieth & Huber, 2013; Salet et al., 2021). In contrast, instructive cueing tasks allow for trial-wise manipulations of attention based on task goals, hence probing the flexible and goal-dependent usage of temporal expectations (Denison et al., 2017, 2021; Fernández et al., 2019; Griffin et al., 2002). Both the automatic utilisation of incidentally learned temporal regularities and flexible, goal-dependent prioritisation are likely to be essential features of how temporal expectations guide behaviour in our dynamically unfolding environments (Nobre & van Ede, 2018).

In the present study, the strengths of both approaches are harnessed by developing a design that encourages goal-dependent usage of contextually embedded temporal expectations to identify targets within extended dynamic backgrounds with pronounced sensory competition. In the present task, participants formed temporal expectations based on the characteristic temporal regularities of stimuli appearing within two rapidly presented concurrent streams. The identity of the relevant target (based on colour or pitch) on any given trial was cued on a trial-by-trial basis to test whether participants could utilise learned temporal regularities flexibly to prioritise the task-relevant stimulus. Importantly, the exact stimulus location (left or right stream) and required response hand were unpredictable and varied trial by trial. Across three experiments, I investigated whether temporal expectation, independent of spatial and motor expectations, facilitated behaviour. To foreshadow the results, visual and auditory temporal expectations were found to be flexibly directed to task-relevant events in the absence of spatial or response-related certainty.

3.3 Experiment 1: visual online study

3.3.1 Methods

3.3.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R73580/RE001). Data were collected from 54 participants recruited through the Prolific Academic platform (https://www.prolific.co). Pre-screening of participants ensured they were aged 18 to 40, fluent in English, had normal or corrected eyesight, and fulfilled specific participation requirements in Prolific Academic. Study inclusion required an approval rate above 95% and participation in at least ten prior experiments. Participants were paid at a rate of £7.50 per hour and received a bonus of up to £2.50, which scaled with performance above 90% accuracy. On average, participants received a bonus payment of £1.50. All participants provided informed consent before beginning the task. To accommodate the additional variability in online testing, the sample size was chosen by doubling the size of the samples used in similar in-person studies of the effects of temporal expectations in extended contexts (i.e., Boettcher et al., 2022).

Data quality in online testing can vary (Sauter et al., 2020), prompting the adoption of strict exclusion criteria. Participants were excluded from further analysis if they performed below 60% accuracy, did not respond to more than 30% of trials, or had mean RTs above 5 SDs from the across-participant mean. Five participants were excluded in total, leaving 49 for analyses (14 female; mean age: 24.75, SD: 7; 8 left-handed).

3.3.1.2 Experimental procedure and stimuli

The experimental script was generated using PsychoPy (PsychoPy Builder v2021.1.4; Peirce et al., 2019) and hosted online through Pavlovia (https://pavlovia.org/; Sauter et al., 2020). Participants completed the study on their personal computers or laptops. Participants were encouraged to use Mozilla Firefox or Google Chrome for this study and asked to keep 60 cm away from their screens. They were not allowed to take part in the study from their phones or tablets. At the beginning of the experiment, participants scaled the image of a credit card to match the size of a physical one which they placed against the screen. This procedure was used to estimate the resolution of their computer screen before starting the experiment (Li et al., 2020). The ratio between the card image width (pixels) and the actual card width (cm) estimated the pixel density (pixel per cm) per participant. Together, this value and the recommended distance from the screen (60 cm) allowed the estimation of the DVA of stimulus presentation.

The task involved identifying one of up to three possible coloured targets that could appear within either of two concurrent rapidly presented streams. Possible targets were coloured circles (green, blue, pink, or yellow), which appeared only once, within either stream, during the trial. Which colour was relevant for the trial was cued by a coloured central cue at trial onset, and participants produced a speeded localisation response by using the equivalent (left vs right) hand upon detecting the relevant target (**Figure 3.1**). Importantly, the location of target appearance (left vs right) was equiprobable and, consequently, the required response hand was also unpredictable. The task was divided into six blocks, each containing 72 trials and lasting ~6 min. Before beginning the first block, participants conducted a practice block of 24 trials. Participants were instructed to rest between blocks. In total, the task lasted around 1 hr.

At the beginning of each trial, a centrally presented cue indicated which of the possible target colours required a response on that trial. The cue was a 250-ms change in the colour of the central fixation cross to match the colour of the designated target. After a 500-ms delay, participants were presented with two streams of coloured and white circles (diameter: 5 DVA). Coloured circles appeared briefly (75 ms) either on the left or on the right side of the screen with a white circle displayed on the opposite side at an estimated distance of 8 DVA from the centre of the screen. Both circles were immediately followed by a bilateral multi-coloured mask, which remained on the screen until the onset of the next coloured circle (**Figure 3.1**).

Each coloured circle within the streams was coloured with one out of four possible colours, which were equidistantly spaced in the CIELab colour space (CIE, 2004; green: #01EB87, orange: #FFAC00, blue: #00E1FF, red: #FF6686). One of these colours was designated as the *distractor* colour, and the other three corresponded to the three possible *target* colours. Designated target and distractor colours were constant within a participant and were counterbalanced across participants. On each trial, participants were cued to identify one out of the three target colours. Thus, only the cued target was task-relevant in each trial, but uncued, task-irrelevant, targets and distractors were also displayed within the streams.

As the main experimental manipulation of temporal expectation, the three targets differed according to *when* they appeared. The temporal predictability of targets was linked to their colour. *Early* targets appeared at a fixed time of 750 ms from stream onset; *late* targets appeared at a fixed time of 1500 ms from stream onset; and *random* targets could appear at any time from stream onset, except for around the *early* (700 – 800 ms) and *late* (1450 – 1550 ms) time points.

Participants responded indicating the location of the circle that matched the cue colour shown at the start of each trial. All circles had an equal probability of appearing on the left or on the right and there was a balanced number of left and right circles in each trial +/- 1. As soon as they detected the target, participants had to press either the left *(f)* or the right *(j)* key corresponding to the location of the target in the left or right stream, respectively. Importantly, because of the dependency between target location and response hand, the required response was random and unpredictable until the target appeared. For target colours with consistent (early or late) temporal onsets, it was hypothesised that participants would incidentally learn the time of target appearance and proactively direct attention to the predicted moment of the target colour to identify target location (left vs right) and generate the correct response (left vs right hand). In contrast, the lack of temporal prediction associated with the randomly timed targets would not support temporally focused proactive attention, resulting in a relative behavioural disadvantage in the detection of randomly timed targets compared to temporally predicted targets.

The streams had a total duration of 2250 ms and did not stop when participants responded. During ITIs (jittered 1750-2000 ms), two placeholder white circles were displayed on the left and the right of the screen. Participants were instructed to keep their eyes on the central fixation cross for the duration of each block.

To minimise the potential effects of foreperiod-linked expectations in the detection of random targets, their onset probability approximated a non-ageing flat distribution (Trillenberg et al., 2000). The absolute likelihood for the random target to appear was 50% during the first third of the trial, 25% in the middle third, and 12.5% in the final third (**Supplementary Figure 7.1**). Thus, as time passed, the conditional probability for the target to occur in each third of the trial, had it not yet appeared (hazard rate), remained at 50%.

In each trial, participants had to respond to the target with the cued colour. Participants were cued to respond to the early, late, and random targets equiprobably (33.3% each; **Supplementary Figure 7.1**). In 37.5% of trials, one of the three targets was absent (12.5% early absent, 12.5% late absent, 12.5% random absent). These trials did not overlap. A third of the trials in each absent category occurred during a trial with a corresponding cue. This resulted in 4.17% of early/late/random trials in which participants were cued on the corresponding target and the target was absent. In these trials, participants were instructed not to respond. Overall, a total of 12.5% of all trials required no response from participants. No-response trials were included to promote participants' engagement in this task and to preserve the non-ageing flat distribution of random target appearance.

All trials contained between 9-12 coloured circles. Most trials contained 3 targets and 6-9 distractors. However, when one of the targets was absent, the trial instead contained 2 targets and 7-10 distractors. The number of distractors was selected randomly from a uniform distribution. To distribute the stimuli equally across the duration of the trial, the streams were segmented into three-thirds. The early target marked the onset of the middle third and the late target marked the onset of the final third. Either 3 or 4 coloured circles appeared in each third. The first circle appearing in each trial was always a distractor and different numbers of stimuli could precede each target, hence minimising any effects of temporal order and emphasizing temporal regularities based on onset timings instead.

Each coloured circle lasted 75 ms. During the ISIs, bilateral circular masks were displayed. ISIs were calculated by choosing pseudo-random numbers from a gamma distribution with a minimum duration of 53 ms, a maximum of 423 ms, and an average of 141 ms, depending on how many stimuli were presented in each third. Twelve unique masks were created by sampling 64x64 elements from a uniform distribution of all target and distractor colours, and one of these masks (chosen randomly) appeared in each trial.

At the end of each trial, participants were provided with written, visual feedback about their performance that was displayed on the centre of the screen. Specifically, participants saw the following message "Correct!" when they correctly detected a target, "Incorrect!" when they pressed the incorrect key, "Too early!" when they pressed before target appearance, "Incorrect! No target present." when they responded in the absence of a target, "Correct! No target present." when they correctly withheld their response in the absence of a target, and "No response given!" when they did not respond in the presence of a target.

At the beginning of the task, participants were shown the three target colours they would need to detect throughout the study. At the end of the session, they were asked to fill in a questionnaire prompting them to report any patterns they had noticed regarding the appearance of the stimuli. Participants had unlimited time to respond using free text. Additionally, participants were shown a horizontal line representing "time in trial" and were asked to place a rectangle at the location on the line that corresponded to the estimated time of target appearance. The horizontal line was divided into 10 bins and participants were asked to report the time of each target's appearance on a different line. The percentage of participants who placed the rectangle on bins 3 or 4 out of 10 when asked about the timing of the early target was calculated. Similarly, the percentage of participants who placed the rectangle on bins 6 or 7 out of 10 when prompted to report the time of late target occurrence was estimated. This approach yielded a chance-level report of target timing of 20%.

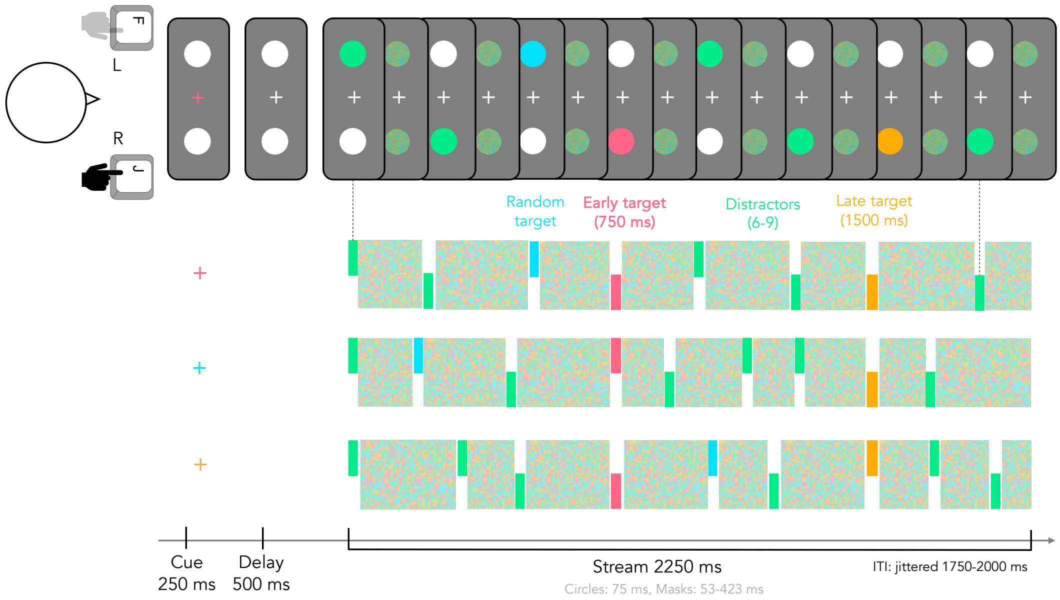


Figure 3.1. Experiment 1: visual online task design. At the beginning of each trial, participants saw a cue (change in the colour of the fixation cross) indicating which of three coloured targets to detect. Participants had to search for a circle with this colour within two streams of successively appearing circles and masks. Unknown to the participants, one of these targets appeared at 750 ms from stream onset (early target), another appeared at 1500 ms from stream onset (late target), and the other could happen at any time (random target). Participants had to respond with the hand corresponding to the side of the trial-designated target.

3.3.1.3 Data analysis and statistical testing

All data analyses were performed using R studio (RStudio Team, 2020). All analyses were performed on trials in which the target stimulus was present. The following trials were excluded from RT analyses: incorrect trials, trials with responses faster than 100 ms, and trials with responses slower than three times the SD of the average RT per participant and condition (early, late, and random) following removal of incorrect trials and trials with RTs faster than 100 ms. After cleaning, an average of 3.43% (SD: 3.54%) trials were removed per participant from the RT analyses.

Two dependent variables were of interest: RT (time from target onset to correct response) and accuracy (proportion of correct responses out of all responses). All analyses compared these measures according to the three conditions: early, late, and random targets. The number of trials in which participants responded when the cued target was absent (i.e., false alarms) was very low (an average of 0.037% of trials; range: 0-0.12%). Consequently, false alarms were not further analysed in the present study.

In a supplementary analysis, reaction time and accuracy were combined into the inverse efficiency score metric (IES; Townsend & Ashby, 1983) to assess the potential effects of a speed-accuracy trade-off on participants' performance over time. The IES is defined as the average reaction time in correct trials divided by the proportion of correct responses per trial and per condition. The IES for early and late targets was calculated per participant and the effect of early/late targets on this metric was assessed with a paired-sample t-test. To calculate the IES to random targets, the time from stream onset until stream offset was divided into 6 time bins ensuring the same number of random targets per bin and the effects of time-in-stream on IES were assessed with an ANOVA (see **Supplementary Figure 7.5**).

Importantly, previous studies have shown that RT and accuracy change as a function of time before target appearance, the foreperiod, with RTs typically decreasing as a function of time (Los, 2010; Luce, 1991; Niemi & Naatanen, 1981). Given that the main distinguishing feature between the three conditions in the task was the time of target appearance (early, late, and random), potential confounds arising from foreperiod effects in the analyses were considered by incorporating the effects of random target onsets on performance in two different ways.

<u>Participant-specific generalised linear modelling, followed by parametric comparisons</u>

For each participant, a GLM was fit (using the *glm* function from *lme4* R package; Version 1.1-30; Bates et al., 2015) to the RTs in response to random targets (assuming a Gamma distribution of RTs and a Gaussian link function; Lo & Andrews, 2015) and to the accuracy of the responses to random targets (assuming a binomial distribution of accuracy and a Gaussian link function). RT and accuracy for random targets was modelled as a linear function of random-target onset time. In participant-specific accuracy GLMs, a Gaussian link function was used when the model converged and, alternatively, a logit link function was chosen in 27 of the models.

From each participant-specific model of performance to random targets, the value of RT and the value of accuracy at the time of early (750 ms from stream onset) and late (1500 ms from stream onset) target appearance was interpolated. Subsequently, the interpolated (or estimated) RT and accuracy values when participants responded to random targets were compared with the actual RT and accuracy values when participants responded to early or late targets. It was hypothesised that participants would be faster and more accurate in responding to temporally predictable targets than would have been estimated based on foreperiod effects alone. To test this hypothesis, I assessed how the factors of predictability (predicted vs random) and time (early vs late) modulated RT and accuracy (actual and estimated) using 2x2 ANOVAs (**Figure 3.2**).

To gauge the consistency of the results in the participant-specific GLMs, the same procedure was repeated using different link functions in supplementary analyses. The relation between RT and random-target onset was tested assuming linear, logarithmic and inverse link functions for all participants and by choosing the best-fitted model (out of the ones above) for each participant (**Supplementary Figure 7.2a,b**). Similarly, participants' accuracy was modelled as a function of random-target onset with four different link functions: linear, logit, cauchit, and the participant-specific best fit (**Supplementary Figure 7.2c,d**). The best-fitted model was identified by selecting the model with the minimal Bayesian information criterion (BIC) and Akaike information criterion (AIC) values.

<u>Generalised linear mixed-effects models</u>

To confirm the reliability of the results, two comprehensive GLMMs were built for RTs and accuracies, respectively. These included condition and target onset as predictors, together with the random effects of participant and target colour.

RT was modelled according to the following formula as implemented in *lmer4*, assuming a gamma distribution of RT and an identity link function between RT and the fixed effects.

*RT ~ 1 + Condition * TargetOnset + (1 + Condition * TargetOnset | Participant) + (1 + Condition * TargetOnset | TargetColour)*

The *Condition* variable had three levels according to the timing of target onset in each trial: early, late, or random. The random condition was used as the reference contrast, ensuring comparison of the early and late conditions to the random condition. Furthermore, adding the *TargetOnset* variable as a predictor captured any variability related to foreperiod effects that might affect the detection of the random target. Consequently, any significant effect of condition on RT would represent effects of visual temporal expectation, above and beyond foreperiod effects and random effects arising from participant and target colour.

Following Matuschek et al.'s (2017) procedure, and with the aim of balancing Type-I errors and power, this maximal model was simplified by eliminating predictors that explained little to no variance until the most parsimonious model remained that did not significantly worsen the model fit:

*RT ~ 1 + Condition * TargetOnset + (1 + Condition * TargetOnset | Participant)*

A similar procedure was followed for accuracy, assuming a binomial distribution of the dependent variable and an identity link function between correctness and the fixed effects:

*Correctness ~ 1 + Condition * TargetOnset + (1 + Condition * TargetOnset | Participant) + (1 + Condition * TargetOnset | TargetColour)*

Like above, this maximal model was simplified by eliminating predictors until the most parsimonious model that fit the data best was left:

*Correctness ~ 1 + Condition * TargetOnset + (1 + Condition * TargetOnset | Participant)*

All models were estimated using a maximum likelihood criterion. The outputs of the models are reported as unstandardised regression coefficients with the t-statistics and the results of two-tailed tests with a 5% criterion for significance.

Due to participant-specific differences in foreperiod effects (e.g., changes in the relation between RT/accuracy and time-in-stream) I decided to base the main interpretations on the participant-specific GLMs and considered the results of the GLMMs as complementary and confirmatory.

3.3.2 Results

The main experimental question concerned whether participants were faster and more accurate at detecting temporally expected targets compared to temporally unexpected targets. Such an effect would indicate benefits of visual temporal expectation in the absence of certainty about stimulus location (left or right stream) or required response (left or right hand). To address this question, RTs and accuracies for the early and late expected targets were compared to the estimated RT and accuracy values at early and late times based on random-target onset (see **Methods**).

A 2x2 ANOVA on response times revealed a main effect of time in trial ($F(1,48) = 27.25$, ***$p < .001$, $\eta^2 = .04$) and a main effect of predictability ($F(1,48) = 9.28$, **$p = .003$, $\eta^2 = .01$) on RT, but no interaction between the factors ($F(1,48) = .06$, $p = .8$, $\eta^2 < .000$; **Figure 3.2a,b**). The main effect of time is suggestive of foreperiod effects in this task, with participants responding faster to late targets than early targets. Additionally, the main effect of predictability indicates that participants were faster at detecting temporally expected targets than temporally unexpected ones.

For accuracy, only a main effect of time was found ($F(1,48) = 15.1$, ***$p < .001$, $\eta^2 = .06$), with no main effect of predictability ($F(1,48) = .78$, $p = .38$, $\eta^2 = .003$) or interaction between the factors ($F(1,48) = .27$, $p = .6$, $\eta^2 = .0003$) (**Figure 3.2c,d**).

Accuracy deteriorated with time in the trial. It was speculated that the absence of effects of temporal predictability on accuracy in the present task may have resulted from the near-ceiling performance of participants, especially, towards the beginning of the streams. A similar pattern of results was observed when fitting the participant-specific GLMs assuming a set of non-linear relations between the dependent variables (RT and accuracy) and target onset (see **Supplementary Figure 7.2**).

To test the presence of systematic changes in performance as a function of time in trial, RT and accuracy were combined into a single measure of IES (Townsend & Ashby, 1983). A paired-samples t-test revealed no differences in IES between early and late targets ($t(48) = 1.47$, $p = .15$, $d = .21$; **Supplementary Figure 7.5**). I additionally divided random targets into 6 time-bins depending on their onset with respect to stream onset and calculated IES per bin and per participant. An ANOVA with bins as a factor revealed a small, yet significant effect of bin on IES ($F(1,48) = 4.36$, $*p = .04$, $\eta^2 = .083$) and a follow-up linear contrast revealed a downwards slope of IES as a function of binned time ($\beta = -.008$, $t = -2.16$, $*p = .03$). From this, it was concluded that time-in-stream changed response properties (i.e., speed-accuracy trade-off) and had a slight effect on overall task performance in Experiment 1 (**Supplementary Figure 7.5**).

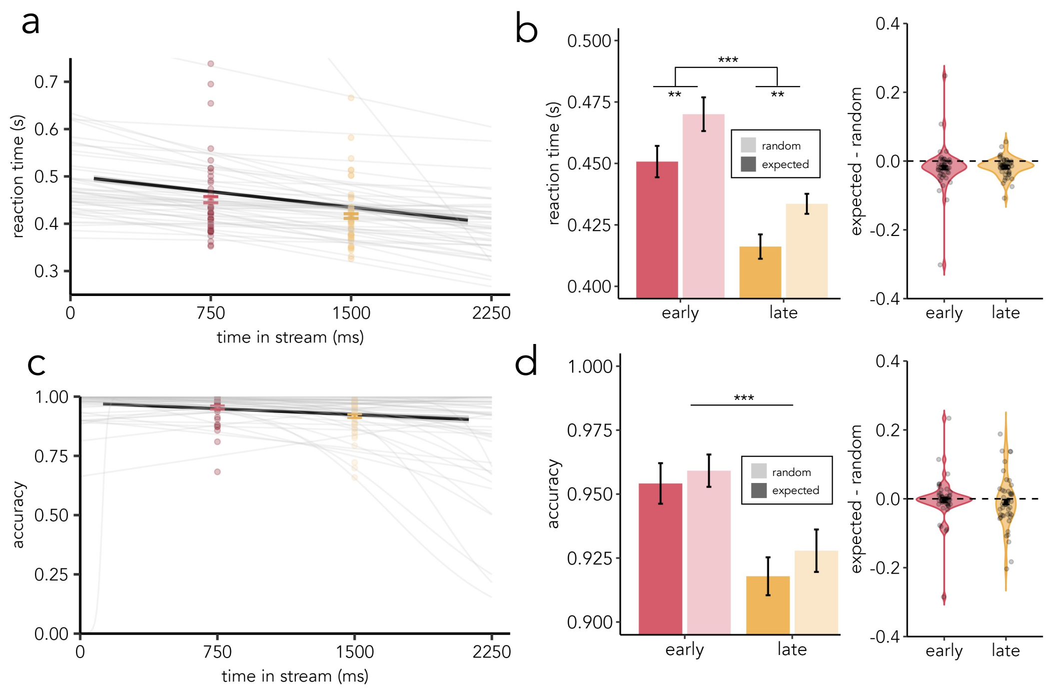


Figure 3.2. Experiment 1: visual online task performance. a) Mean RT to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual RT to early (pink) and late (yellow) targets across participants. b) Left: average RT to expected targets and average RT to random targets (as estimated by participant-specific GLMs). Right: difference between RT at the time of early/late target as estimated from participant-specific GLMs and actual RT to early/late targets. c) Mean accuracy to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual accuracy to early (pink) and late (yellow) targets across participants. d) Left: average accuracy to expected targets and average accuracy to random targets (as estimated by participant-specific GLMs). Right: difference between accuracy at the time of early/late target as estimated from participant-specific GLMs and actual accuracy to early/late targets. Error bars represent SEM, pink represents early time, yellow represents late time, lighter colours represent the values estimated based on participant-specific GLMs and darker colours represent actual values. Individual participants' differences are depicted by dots and dashed lines represent 0 (no difference). Statistical significance is indicated with asterisks.

Similar results were obtained when fitting the dependent variables in two exhaustive GLMMs that considered RT (*early*: β = -.022, t = -1.56, p = .12; *late*: β = -.019, t = -3.22, **p = .001) and accuracy (*early*: β = .023, z = .26, p = .79; *late*: β = -.07, z = -.84, p = .4) as the dependent variables and participants as a random effect (see **Methods**). The small disparities observed in the results revealed by each statistical approach likely arise from differences in how participant-specific effects are integrated and considered in each kind of model. While GLMMs are a powerful method for integrating single-trial variables into a model, they may not explicitly consider participant-specific differences in performance (e.g., participant-specific changes in the relation between the dependent variables RT/accuracy and time-in-stream), which may contribute to the present differences. Due to their sensitivity to participant-specific performance patterns, the conclusions are based on the results of the participant-specific GLMs while the GLMMs serve to provide supplementary confirmation.

In the post-experiment questionnaire, three participants out of forty-nine reported having noticed that some target colours appeared closer to the onset and others closer to the offset of the streams. When prompted to place a vertical bar on a horizontal line depicting "time in trial", 18% of the participants placed the early target colour around the time of its appearance and 13% of the participants placed the late colour correctly. Chance level placement would occur on 20%. This suggests that, for most participants, temporal regularities within the trial were learned incidentally and benefited performance implicitly, without their explicit knowledge.

3.4 EXPERIMENT 2: VISUAL IN-PERSON STUDY

The second experiment was aimed at replicating the results from Experiment 1 during in-person testing and after introducing minor modifications to improve task sensitivity and offer generalisation. Specifically, the difficulty of the task was increased to enhance the variability of participants' accuracies and thereby optimise the design to investigate any potential effects on target detection accuracy. Additionally, to ensure that the results found in Experiment 1 were not tied to the specific choices of colours and timings, four different colours and slightly different stimulus durations and stream timings were used in Experiment 2.

3.4.1 Methods

3.4.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R76234/RE001). Due to reports of varying data quality in online experiments (Sauter et al., 2020), the sample size was reduced from Experiment 1 to Experiment 2. The sample size was chosen based on the effect sizes reported in similar studies exploring the effects of temporal expectations in dynamic and extended contexts (i.e., Boettcher et al., 2022). Data was collected from 24 participants recruited through the Oxford Psychology Research (OPR) participant recruitment scheme. Pre-screening of participants ensured they were aged 18 to 40, fluent in English, had normal or corrected eyesight and hearing, were not taking psychoactive medication, and had no history of severe neurological or psychiatric disorders. Participants were paid at a rate of £10 per hour. All participants provided informed consent prior to beginning the study. Using the same participant exclusion criteria as above, one participant was excluded from further analyses, leaving 23 for analyses (11 female; mean age: 25.96, SD: 3.4; 5 left-handed).

3.4.1.2 Experimental procedure and stimuli

The experimental script was generated using PsychoPy (PsychoPy Builder v2021.1.4; Peirce et al., 2019). To perform the task, participants were placed 60 cm away from a monitor [22-inch (55.88 cm) Samsung SyncMaster 2233; resolution, 1680 × 1050 pixels; refresh rate, 100 Hz; screen width, 47 cm].

The stimuli and experimental procedures were the same as those in Experiment 1, with the following differences (**Figure 3.3**). To make the task more difficult, the timings of the stimuli were shortened. The duration of the streams was 1500 ms, with the early target appearing at 500 ms and the late target appearing at 1000 ms from stream onset. All coloured circles (targets and distractors) appeared for 50 ms, and the ISIs (masks) lasted a minimum of 45 ms and a maximum of 350 ms (centred on a mean duration of 130 ms). The masks were created by sampling 16x16 elements from a uniform distribution of target and distractor colours and white, thus amplifying their masking effect. To ensure that the results found in Experiment 1 did not depend on specific colours, four slightly different, also highly distinguishable colours (green: #00ED82, orange: #FFAC00, pink: #FF62FF, blue: #00DEFF) were chosen for Experiment 2.

Experiment 2 was divided into 8 blocks, each containing 72 trials and lasting ~5 min. The first block provided participants with a chance to practice the task. Participants were instructed to rest between blocks. The task lasted around 1 h in total. At the end of the session, participants were asked to report any patterns they had noticed regarding the appearance of the stimuli but were not prompted to provide more details as in Experiment 1.

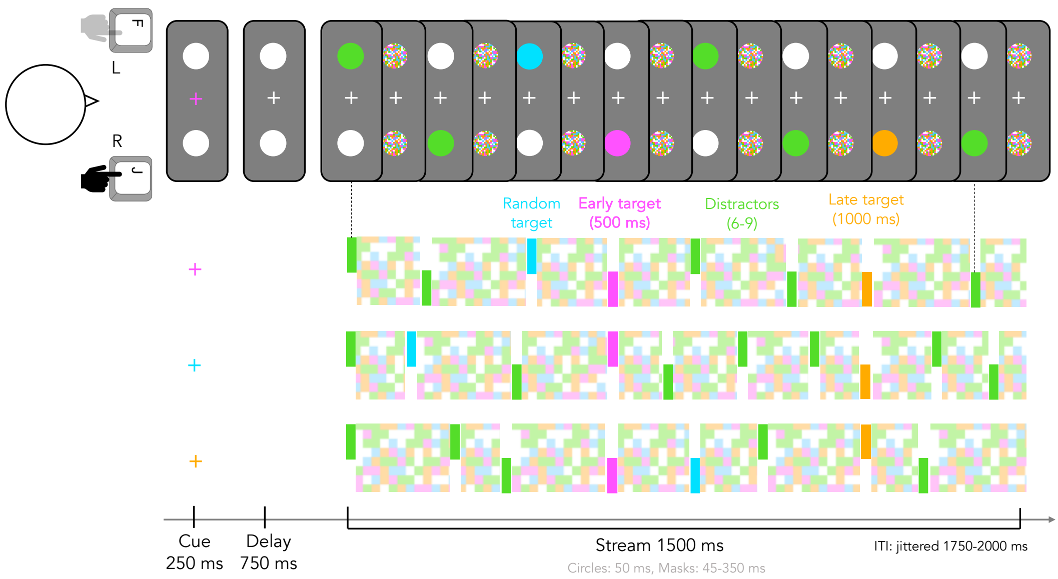


Figure 3.3. Experiment 2: visual in-person task design. At the beginning of each trial, participants saw a cue (change in the colour of the fixation cross) indicating which of three coloured targets to detect. Participants had to search for a circle with this colour within two streams of successively appearing circles and masks. Unknown to the participants, one of the coloured targets appeared at 500 ms from stream onset (early target), another appeared at 1000 ms from stream onset (late target), and the other could happen at any time (random target). Participants had to respond with the hand corresponding to the side of the trial-designated target.

3.4.1.3 Data analysis and statistical testing

Data analysis followed the same procedures as in Experiment 1. An average of 2.05% (SD: 2.27%) trials were removed per participant for the RT analyses. An average of 0.017% of trials (range: 0.002-0.09%) constituted false alarm trials and these were not further analysed.

3.4.2 Results

As in Experiment 1, the hypotheses in Experiment 2 pertained to whether participants' performance would be improved by the temporal predictability of the targets embedded within the streams.

To address this question, RT and accuracy values at the expected target times were estimated based on the random-target onsets and compared to the actual RT and accuracy values for early and late targets across participants. A 2x2 ANOVA revealed a main effect of time ($F(1,22) = 9.47$, $^{**}p = .006$, $\eta^2 = .037$) and a main effect of predictability ($F(1,22) = 6.43$, $^{*}p = .02$, $\eta^2 = .038$) on RT, and a trend towards an interaction between the factors which did not reach statistical significance ($F(1,22) = 3.9$, $p = .06$, $\eta^2 = .008$; **Figure 3.4a,b**). Additionally, there was a main effect of both time ($F(1,22) = 5.64$, $^{*}p = .03$, $\eta^2 = .043$) and predictability ($F(1,22) = 5.56$, $^{*}p = .03$, $\eta^2 = .076$) on accuracy but no interaction between the factors ($F(1,22) = .02$, $p = .88$, $\eta^2 < .000$; **Figure 3.4c,d**). From this, it was concluded that participants were faster and more accurate at detecting temporally expected targets than temporally unexpected ones.

Across the trial duration, performance became faster but less accurate for long compared to short target onsets. To investigate potential changes to performance as a function of time, IES was calculated for early and late targets and no evidence for statistically significant differences between conditions was found ($t(22) = -.62$, $p = .52$, $d = .14$). Additionally, an ANOVA of random target IES with bins as factors showed that there were no differences in IES as a function of time in stream (F(1,22) = .43, p = .52, η^2 = .02; **Supplementary Figure 7.5**). From this, it was concluded that overall performance did not change systematically over time in Experiment 2.

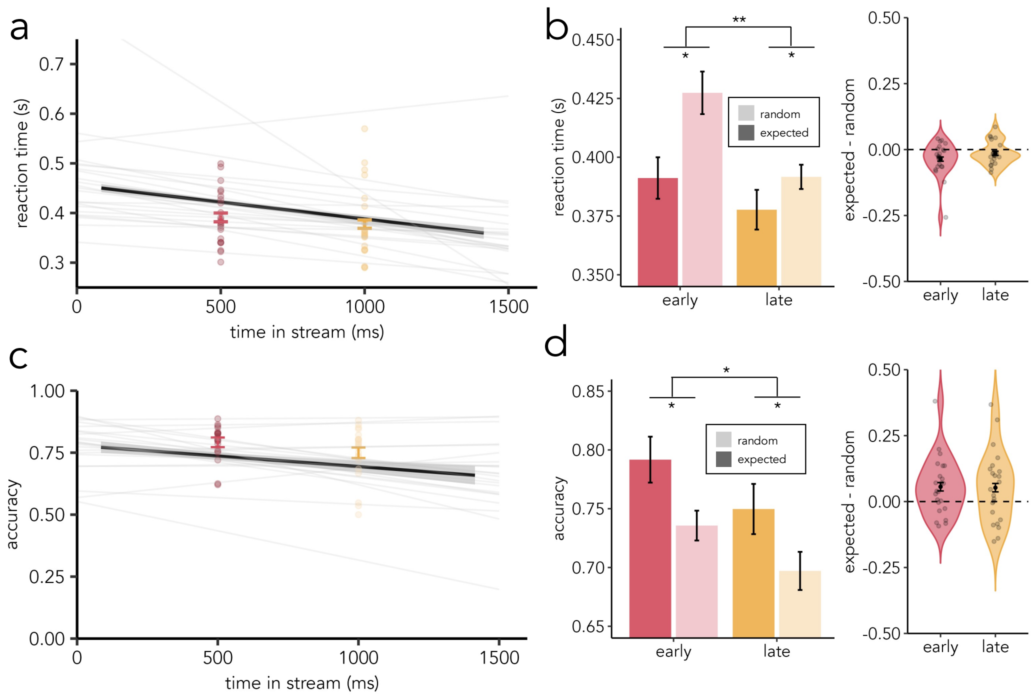


Figure 3.4. Experiment 2: visual in-person task performance. a) Mean RT to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual RT to early (pink) and late (yellow) targets across participants. b) Left: average RT to expected targets and average RT to random targets (as estimated by participant-specific GLMs). Right: difference between RT at the time of early/late targets as estimated from participant-specific GLMs and actual RT to early/late targets. c) Mean accuracy to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual accuracy to early (pink) and late (yellow) targets across participants. d) Left: average accuracy to expected targets and average accuracy to random targets (as estimated by participant-specific GLMs). Right: difference between accuracy at the time of early/late targets as estimated from participant-specific GLMs and actual accuracy to early/late targets. Error bars represent SEM, pink represents early time, yellow represents late time, lighter colours represent the values estimated based on participant-specific GLMs and darker colours represent actual values. Individual participants' differences are depicted by dots and dashed lines represent 0 (no difference). Statistical significance is indicated with asterisks.

These results were similar in participant-specific GLMs with non-linear link functions (see **Supplementary Figure 7.3**) and in two exhaustive GLMMs for RT (*early*: β = -.042, t = -2.19, *p = .03; *late*: β = -.013, t = -.93, p = .35) and accuracy (*early*: β = .056, z = 2.55, *p = .01; *late*: β = -.053, t = 1.92, p = .06). The small disparities observed in the results revealed by each statistical approach likely arise from differences in the treatment of participant-specific effects in each kind of model. In the post-task debriefs of Experiment 2, no participants reported being aware of the regularities.

In Experiment 2, the main pattern of findings from Experiment 1 was replicated. Namely, visual temporal expectation facilitated performance despite spatial uncertainty and when participants were unable to prepare one action. Therefore, the effects generalised across online vs in-person testing conditions, stimulus timings, stimulus colours, and task difficulty. Furthermore, increasing the demands of stimulus presentation parameters in Experiment 2 revealed that the effects of visual temporal expectation occurred both in participants' reaction times and accuracies.

3.5 EXPERIMENT 3: AUDITORY IN-PERSON STUDY

The third experiment was aimed at testing the generalisability of the previous results to other sensory modalities and, more specifically, to audition. Therefore, the experimental design was translated from the visual to the auditory modality while keeping most experimental parameters as similar as possible.

3.5.1 Methods

3.5.1.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R76234/RE001). The sample size was chosen based on the effect sizes in Experiment 2. Data were collected from 30 participants recruited through the OPR participant recruitment scheme. Pre-screening of participants ensured they were aged 18 to 40, fluent in English, had normal or corrected eyesight and hearing, were not taking psychoactive medication, and had no history of severe neurological or psychiatric disorders. Participants were paid at a rate of £10 per hour. All participants provided informed consent before the study. Given the lower mean accuracy and higher accuracy variability observed in Experiment 3, participant exclusion criteria were adapted accordingly. Specifically, participants whose average accuracy was below 55% and who did not respond to more than 30% of trials were removed from further analyses. Other participant exclusion criteria were as in Experiment 2. In total, three participants were excluded from further analyses, leaving a sample size of 27 participants (17 female and 10 male; mean age: 20.05, SD: 3.08; 3 left-handed).

3.5.1.2 Experimental procedure and stimuli

The experimental script was generated using the Psychophysics Toolbox version 3.0.18 (Brainard, 1997) on Matlab 2022a (The Mathworks Inc., Natick, NA, USA). The task was displayed on a monitor (Dell U2312HM; 1920x1080 pixels resolution; 100 Hz refresh rate) while participants sat ~60 cm away from it. Participants wore Beats EP ® wired headphones (model A1746) for the duration of the study. All sounds were played at a sampling rate of 48 kHz. The experimental procedure and stimulus timings were the same as those in Experiment 2 with the key difference that the lateralised coloured circles (targets) were replaced with pure tones of different pitches which were played over the left and right ear.

The task involved identifying one of up to three possible pure tones (targets) that could be played within either of two streams of tones which were concurrently played on each ear. Possible targets were pure tones (600 Hz, 896 Hz, 1339 Hz, and 2000 Hz) which were played once within either stream. The relevant tone for each trial was cued by playing a matching pure tone binaurally at trial onset, and participants produced a speeded localisation response by using the corresponding (left vs right) hand upon hearing the relevant target (**Figure 3.5**). The ear to which the target tone was played was equiprobable and, consequently, the required response hand was unpredictable. The task was comprised of 8 blocks, each containing 72 trials and lasting ~5 min. Participants were allowed to rest between blocks. The first block was a practice block to become accustomed to the procedure and was not included in further analyses.

At the beginning of each trial, a pure tone was played binaurally for 250 ms (cue), indicating which of the possible target tones required a response on that trial. Following a 750-ms delay, pure tones interspersed within two streams of white noise were played through the headphones. Volume was kept constant across participants (50% of the computer's audio-device volume) and tones of different frequencies were matched in loudness using the ISO226 Equal-Loudness-Level Contour Signal (Tackett, 2024). Each tone was played for 50 ms and had two Gaussian ramps at the beginning and the end (5 ms long each). Each of the tones was played either on the left or the right ear while nothing was played on the opposite ear. Each tone was immediately followed by a binaural white noise mask, which was played until the onset of the next pure tone.

Each pure tone in the stream had a pitch matching one out of four logarithmically equidistant frequencies: 600 Hz, 896 Hz, 1339 Hz, and 2000 Hz. One of these tones was designated as the *distractor* tone and the other three corresponded to the three possible *target* tones. In contrast to Experiments 1 and 2, in Experiment 3, only the two middle frequencies were ever chosen as distractors (896 Hz and 1339 Hz). This was aimed at equalising the distance between the distractor tone and the three possible target tones, a factor which is known to affect discriminability of pure tones (Levitt, 1971). Designated target and distractor tones were constant within a participant and counterbalanced across participants. Importantly, a white fixation cross was shown in the centre of the screen throughout the task, thus encouraging participants to fixate on the centre.

On each trial, participants were cued to identify one out of the three target tones (task-relevant) but uncued, task-irrelevant targets and distractors were also played. Crucially, the three target tones of distinct frequencies also differed in their timings. Like Experiments 1 and 2, the three target tones differed according to *when* they were played, and the temporal predictability of targets was linked to their pitch. *Early* targets were played at a fixed time of 500 ms from stream onset; *late* targets were played at a fixed time of 1000 ms from stream onset; and *random* targets could be played at any time from stream onset, except for around the *early* (400 – 600 ms) and *late* (900 – 1100 ms) time points. All tones had an equal probability of being played on the left and on the right and there was a balanced number of left and right tones in each trial +/- 1.

Following the procedure detailed in Experiments 1 and 2, random target onset probability had a non-ageing flat distribution (Trillenberg et al., 2000). The proportion of cued and absent trials, as well as the number of tones per stream were identical to what was previously described. The number of tones (targets and distractors) played across both streams was the same as in Experiments 1 and 2 (9-12 tones with mostly 3 targets and 6-9 distractors). The ITI was randomly sampled from a uniform distribution between 1000 ms to 1250 ms and other timings (e.g., stream duration) were identical to those in Experiment 2.

At the beginning of the task, participants were played the three target tones they would need to detect throughout the study. At the end of the session, they were informally asked about any patterns that they had noticed regarding the appearance of the stimuli.

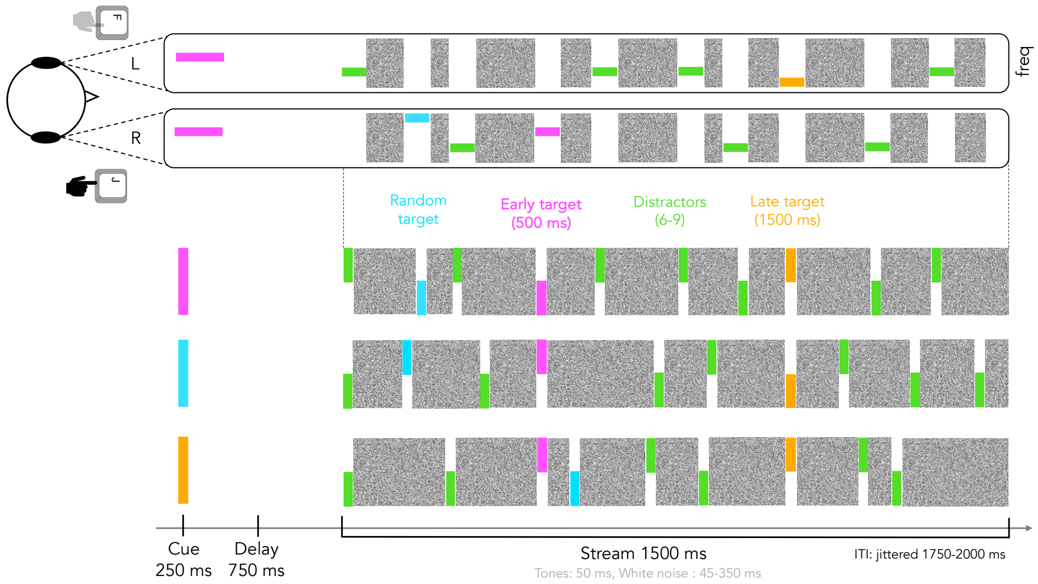


Figure 3.5. Experiment 3: auditory in-person task design. At the beginning of each trial, participants heard a pure tone binaurally (cue) indicating which of three pure tones (targets) to detect. Participants had to search for a pure tone with the cue-matching pitch within two auditory streams of successive pure tones (monaural) intercalated with white noise (binaural). Unknown to the participants, one of the tones was played at 500 ms from stream onset (early target), another was played at 1000 ms from stream onset (late target), and the other could happen at any time (random target). Participants had to respond with the hand corresponding to the side on which the target tone was played.

3.5.1.3 Data analysis and statistical testing

Data analysis followed the same procedure as in Experiments 1 and 2. An average of 1% (SD: 0.63%) of trials were removed per participant from the RT analyses. An average of 4.37% of trials (range: 0-8.33%) constituted false alarm trials, and these were not further analysed.

The most parsimonious GLMMs that did not significantly worsen the model fit in Experiment 3 were the following:

$$RT \sim 1 + Condition + TargetOnset + (1 + Condition + TargetOnset \mid Participant)$$

$$Correctness \sim 1 + Condition + TargetOnset + (1 + Condition + TargetOnset \mid Participant)$$

3.5.2 Results

As in Experiments 1 and 2, the hypotheses in Experiment 3 pertained to whether participants' performance would be improved by the temporal predictability of the targets embedded within the auditory streams.

RT and accuracy at the expected times were estimated based on the random-target onsets and they were compared to the actual RT and accuracy values for early and late targets across participants. A 2x2 ANOVA revealed a main effect of time ($F(1,26) = 53.17$, $***p < .001$, $\eta^2 = .15$) and a main effect of predictability ($F(1,26) = 5.7$, $*p = .02$, $\eta^2 = .014$) on RT, but no interaction between the factors ($F(1,26) = .15$, $p = .7$, $\eta^2 < .000$; **Figure 3.6a,b**). Additionally, there were no main effects of time ($F(1,26) = .02$, $p = .9$, $\eta^2 < .000$) nor predictability ($F(1,26) = 2.37$, $p = .14$, $\eta^2 = .023$) on accuracy and no interaction between the factors ($F(1,26) = .01$, $p = .73$, $\eta^2 < .000$; **Figure 3.6c,d**). From this, it was concluded that participants were faster but not more accurate at detecting temporally expected tones than temporally unexpected ones.

These results were confirmed in participant-specific GLMs with non-linear link functions (see **Supplementary Figure 7.4**) and in two exhaustive GLMMs for RT (*early*: $\beta = -.068$, $t = -1.7$, $p = .09$; *late*: $\beta = -.049$, $t = -2.32$, $*p = .02$) and accuracy (*early*: $\beta = .27$, $z = 1.22$, $p = .22$; *late*: $\beta = .43$, $t = 1.7$, $p = .09$).

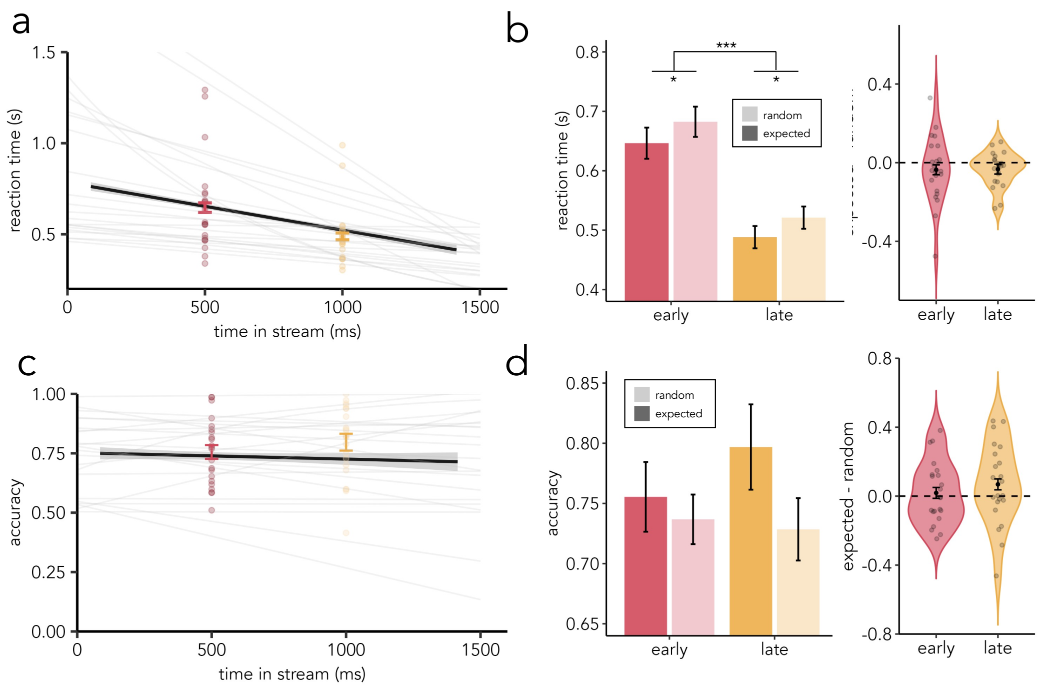


Figure 3.6. Experiment 3: auditory in-person task performance. a) Mean RT to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual RT to early (pink) and late (yellow) targets across participants. b) Left: average RT to expected targets and average RT to random targets (as estimated by participant-specific GLMs). Right: difference between RT at the time of early/late targets as estimated from participant-specific GLMs and actual RT to early/late targets. c) Mean accuracy to random targets as a function of target onset as estimated by participant-specific GLMs (thin grey lines) and actual accuracy to early (pink) and late (yellow) targets across participants. d) Left: average accuracy to expected targets and average accuracy to random targets (as estimated by participant-specific GLMs). Right: difference between accuracy at the time of early/late targets as estimated from participant-specific GLMs and actual accuracy to early/late targets. Error bars represent SEM, pink represents early time, yellow represents late time, lighter colours represent the values estimated based on participant-specific GLMs and darker colours represent actual values. Individual participants' differences are depicted by dots and dashed lines represent 0 (no difference). Statistical significance is indicated with asterisks.

Across trial duration, performance became faster for long compared to short target onsets. To investigate potential changes to performance as a function of time, IES was calculated for early and late targets and evidence for statistically significant differences between conditions was found ($t(26) = 3.34$, $^{**}p = .002$, $d = .64$). Additionally, an ANOVA of random target IES with bins as factors showed that there were differences in IES as a function of time in stream ($F(1,26) = 24.63$, ***$p < .001$, $\eta^2 = .49$; **Supplementary Figure 7.5**). From this, it was concluded that overall performance changed systematically over time in Experiment 3, such that participants became better (lower IES values) over time. Given that no general decreases in accuracy were found as a function of time-in-stream, this was interpreted as mostly driven by RT. At the end of the session, three participants reported having noticed a similar "melody" and two participants correctly identified that some tones had been played towards the beginning or the end of the stream. Therefore, there may have been explicit awareness of the temporal regularities in the task in some, but probably not all participants.

Together, Experiment 3 generalised the main findings from Experiments 1 and 2 to the auditory modality. Both visual and auditory attention could be flexibly directed to temporally expected features in the absence of spatial and motor certainty. Despite similar average accuracies in Experiments 2 and 3, Experiment 3 only found differences in participants' RT as a function of temporal predictability, suggesting that the mechanisms underlying task performance may have differed from the visual to the auditory modality.

3.6 DISCUSSION

The present study shows that expectations arising from incidentally learned temporal regularities can guide behaviour in a flexible, goal-driven manner, even in the absence of spatial and motor certainty. This finding was replicated across three experiments that differed in sensory modality (visual vs auditory), stimulus timings, difficulty, and testing modality (online vs in-person). Across all experiments, temporal expectation influenced participants' reaction times. Following an increase in task difficulty in Experiments 2 and 3, the behavioural benefit of visual, but not auditory, temporal attention was evident in accuracy measures. Performance benefits from temporal expectations in all experiments surpassed and did not interact with behavioural effects related to the passage of time in a trial (foreperiod).

It has previously been proposed that attention based on temporal expectation must act through other stimulus attributes, in the case of visual temporal attention particularly through space and, in visual and auditory temporal attention, also through motor processes (e.g., Morillon et al., 2015; Salet et al., 2021; Thomaschke & Dreisbach, 2013). Most studies to date have investigated temporal attention under spatial or motor certainty. Investigating the co-dependence of spatial and temporal expectation specifically, Rohenkohl and colleagues (2014) simultaneously cued a location (left vs right) and a temporal interval (short vs long) in each trial and found that behavioural benefits of visual temporal expectation were restricted to the attended location (see also Doherty et al., 2005; Seibold et al., 2020).

In contrast, in this task, no spatial certainty was required to express the benefits of temporal expectation. Here, temporal predictability was linked to stimulus colour/pitch while remaining decoupled from stimulus location and motor response. The spatially distributed nature of the benefits conferred by combined colour-temporal and pitch-temporal predictions suggests that temporal regularities can also tune feature-based attention (Cohen & Maunsell, 2011; Gabay & Henik, 2010; Kingstone, 1992; Maunsell & Treue, 2006; Pratt & Abrams, 1999; Thomaschke et al., 2016; Wagener & Hoffmann, 2010b; Warren et al., 2014). Speculatively, temporal expectations could latch onto different types of top-down attentional signals, including spatially distributed feature-based representations, and not necessarily require full spatial or motor certainty.

From a neural perspective, temporal expectations have been suggested to exert their effects by amplifying neural motor and/or perceptual representations at specific times (Nobre & Rohenkohl et al., 2014; Nobre & van Ede, 2018). Preparatory motor responses have repeatedly been shown to change with temporal expectancy (Boettcher et al., 2021; Calderon et al., 2018; Cisek, 2007; Heideman, et al., 2018, 2018a, 2018b; Miniussi et al., 1999; Thomaschke & Dreisbach, 2013; Trillenberg et al., 2000; van Ede et al., 2020; van Elswijk et al., 2007; Wang et al., 2020).

In the visual domain, temporal expectation has been shown to modulate neuronal firing based on sensory and sensorimotor spatial receptive fields (Ghose & Maunsell, 2002; Janssen & Shadlen, 2005), as well as other visual features (Warren et al., 2014; Anderson & Sheinberg, 2008). Similarly, in the auditory domain, the frequency tuning of rodent auditory cortex neurons is known to be modulated by temporal expectations (Jaramillo & Zador, 2011). In all these studies, however, stimuli were spatially certain. The present results suggest that temporal expectation can equally modulate top-down attentional biases of non-spatial features such as colour and pitch. A related observation was that by Lima and colleagues (2011). In their study, NHPs temporally anticipated a centrally presented grating. Neuronal modulation of orientation-specific activity by temporal expectation extended beyond the spatial confines of the fovea representation, possibly reflecting how temporal predictions interact with a spatially distributed representation of orientation. In addition to modulating neural representations over at least two locations, the results of the present study speculatively suggest that temporal expectations can increase temporal preparedness for two different actions simultaneously (see also Calderon et al., 2018; Cisek, 2007; Kornysheva et al., 2013; Wang et al., 2020).

In this task, target locations and corresponding responses were simple and not in strong competition; the two locations were in different hemifields or ears, and the two responses engaged different hands. It will be important to investigate whether benefits from temporal orienting of attention still occur under greater spatial and motor ambiguity or competition. It remains possible that temporal expectation is confined to influencing non-competing spatial or motor representations that can be activated concurrently to guide task performance. In addition, spatial or motor factors may interact strongly with other non-spatial factors in setting proactive expectations and set limits to how learned temporal structures can influence the resulting top-down attentional signals.

Most of the literature investigating attention has focused on the visual domain. While the basic principles have been considered to be generalisable across sensory systems, several differences between visual and auditory attention have also been noted (for reviews see Noyce et al., 2023; Shinn-Cunningham & Best, 2008). While visual features are encoded spatially, auditory information is expressed over time and the location of an auditory source is estimated at later processing stages by comparing the time at which a sound reaches each ear (e.g., Musiek & Chermak, 2015). Consistently, directing attention to the location of a sound has been suggested to engage a visual attention system, and orienting attention to the time of visual events seems to activate an auditory system instead (Lee et al., 2012; Michalka et al., 2015, 2016). Interestingly, in the present study, both visual and temporal attention were found to facilitate performance in the absence of spatial and motor-related certainty through similar effects on reaction time. Using this design, future studies could directly compare the modulatory effects of attention on visual features such as colour and auditory features such as pitch.

An innovative aspect of the present design is the orthogonal manipulation of task relevance (task-relevant and task-irrelevant targets) and temporal expectations (early, late, and random; see also Duyar et al., 2023). Most informative cueing studies of temporal attention manipulate expectations by changing the probability of target appearance (e.g., Coull & Nobre, 1998; Miniussi et al., 1999). In contrast, here, task goals were manipulated on a trial-by-trial basis, such that all or most targets were present in any given trial, but only one was relevant to the task at hand (see also Denison et al., 2017, 2021; Fernández et al., 2019; Griffin et al., 2002).

In real-world contexts, goals and contextual regularities work together to guide attention proactively. Yet, experimentally, the deployment of attention based on goals (e.g., Griffin et al., 2002) or contextual regularities (e.g., Olson & Chun, 2001) have been investigated separately using distinct task designs. This mixed design brings the two types of guidance signals together: expectations result from incidentally learned temporal structures and goals determine their flexible utilization.

While this study suggests that a combination of contextual temporal expectations and task goals can guide behaviour, it does not elucidate how they operate together to guide attention. For example, the present studies are uninformative regarding the extent to which temporal expectations modulate processing of predictable but task-irrelevant targets. In the future, this task design could be combined with continuous and time-resolved metrics such as gaze and pupil size (see Denison et al., 2019, 2020; Palmieri et al., 2023), and neurophysiological measures of anticipation (e.g., CNV, alpha power) and stimulus processing (e.g., P1, N2PC, P300, decoding of target colour), to probe how temporal regularities enhance and/or inhibit the processing of goal-relevant and goal-irrelevant events over time.

Furthermore, the mechanisms whereby temporal regularities are learned and used to guide visual attention in the present task require further study. Participants likely formed associations between specific colours/pitches and moments in time, which in turn facilitated target identification and localisation to select the appropriate response (see also Chun & Jiang, 1998; Zhao et al., 2013). From a neural perspective, the incidental learning of temporal structure through statistical regularities may include visual areas interacting with the basal ganglia, the cerebellum and/or the hippocampus-based learning systems (e.g., Breska & Ivry, 2016; Chun & Phelps, 1999; Covington et al., 2018; Goldfarb et al., 2016; Turk-Browne et al., 2009).

Other than their online vs in-person implementation, the main difference between Experiments 1 and 2 was the increased temporal competition and resulting task difficulty of the latter. This resulted in accuracy improvements for identifying temporally expected targets. Some studies have suggested that the speeding of responses caused by temporal expectations is reflective of modulations in preparatory motor activity, whereas changes in accuracy reflect influences on perceptual processes (e.g., Tal-Perry & Yuval-Greenberg, 2022). In the context of the present task, this would speculatively point to a modulation by visual attention of both motor and perceptual processes when task difficulty is sufficiently high (see also Kingstone, 1992). Interestingly, despite similar average accuracies in Experiments 2 and 3, auditory temporal attention did not improve pitch detection accuracy. This may be the product of a larger variability in participants' identification of pitch as opposed to colours, but it might also reflect underlying differences in the modulatory effects of auditory and visual attention. Titrating what stages of processing (sensory, associative, or motor) contribute to the present behavioural effects would benefit from using additional appropriate psychophysical methods (e.g., signal detection theory, theory-of-visual-attention modelling, e.g., Vangkilde et al., 2013) and electrophysiological measures.

Investigating cognitive processes unfolding in extended contexts brings along difficulties. The passage of time (foreperiod) may drive expectation and/or change the level of non-specific motor preparation or arousal, hence resulting in systematic changes to the behavioural metrics of interest (Los, 2010; Luce, 1991). Like previous studies, I sought to reduce foreperiod-related effects by keeping the conditional temporal probability of random targets appearing fixed at 50% in each successive third. Foreperiod effects were nevertheless present in the behavioural metrics of this baseline condition. Understanding the source of the foreperiod effect under such controlled conditions is of intrinsic interest and deserves investigation. In this case, the foreperiod effect was modelled by capitalising on the temporal spread of random target appearance to isolate the benefits of temporal attention above and beyond the foreperiod effects.

The complications observed in dynamic tasks tap into the nuances of natural behaviour unfolding in real-world contexts, where several dimensions of temporal flux co-exist and interact (Nobre & van Ede, 2023). These results highlight the need to develop dynamic, ecologically valid designs in which foreperiod effects and other kinds of temporal expectations co-occur and simultaneously influence behaviour.

Taken together, the present results show that visual and auditory temporal expectations formed from incidentally learned temporal regularities can be called upon flexibly, in a goal-driven manner, to guide behaviour. Moreover, I find that temporal attention can facilitate performance in the absence of concomitant spatial or motor expectations in dynamically unfolding environments. Importantly, this was the case both in the visual and auditory modality. Combining this task design with continuous behavioural and neurophysiological measures can pave the way to a better understanding of temporal attention.

4 TEMPORAL REGULARITIES TUNE THE PRIORITISATION OF WORKING-MEMORY CONTENTS

4.1 ABSTRACT

Internal selective attention prioritises working-memory contents to prepare us for prospective behaviours. The prioritisation of visual contents in working memory is flexible and temporally tuned. In addition to visual contents, action-related contents can also be prioritised in working memory, highlighting the pragmatic nature of internal attention. An open question is whether the prioritisation of action-related contents is similarly flexible and tuned to the temporal structure of the task. Additionally, it is unclear if the modulation of co-existing sensory and action-related contents in working memory is intrinsically coupled. In Experiment 1, I designed a task that encourages the flexible prioritisation of two item locations and two associated prospective actions as a function of dynamically evolving temporal expectations. The design orthogonally manipulated item location (left vs right side) and prospective action (left vs right hand), enabling the independent tracking of the prioritisation of sensory contents (through alpha EEG activity modulation and gaze biases) and prospective actions (through mu-beta EEG activity changes). Results across two sessions showed that sensory- and action-related prioritisation co-exist in working memory. Both are flexible and temporally tuned, as indexed by reaction-time benefits,

modulations in alpha and mu-beta EEG activity, and shifts in gaze biases. Interestingly, modulations of visual and action signals were not continuously temporally coupled. The findings highlight a variety of modulatory processes that co-occur to prepare internal representations for adaptive behaviour.

Most studies have manipulated the prioritisation of contents in visual working memory. While it is thought that the basic principles are generalisable to other sensory modalities, the flexibility and temporal tuning of the prioritisation of auditory contents in working memory have not been probed. In Experiment 2, I translated the key features of the task design in Experiment 1 to address this question. Reaction times revealed that the prioritisation of auditory contents was similarly flexible and temporally tuned. Nevertheless, it was not accompanied by content-specific biases in gaze position. These findings point to at least partially non-overlapping mechanisms for the prioritising visual and auditory working-memory contents, which merit further investigation.

4.2 Experiment 1: visual

4.2.1 Introduction

Internal selective attention serves to select and prioritise working-memory contents according to goals, expectations, and other control-related cognitive processes (Myers et al., 2017; Nobre, 2018; Nobre & van Ede, 2023; Oberauer, 2019; Oberauer & Hein, 2012; van Ede & Nobre, 2023). Far from changing randomly, our environment is highly structured across space, time, and several other attributes (e.g., Schwartz et al., 2007). Internal attention is thought to use these regularities to prioritise working-memory contents and, thereby, proactively guide ongoing behaviour.

Numerous studies have found that expectations about the sensory qualities of objects (i.e., location, colour, and other stimulus features) can proactively guide internal attention to the relevant working-memory contents thus facilitating subsequent task performance (Griffin & Nobre, 2003; Landman et al., 2003; Lewis-Peacock et al., 2012; Oberauer & Hein, 2012; Serences et al., 2009; for reviews see Souza & Oberauer, 2016; van Ede & Nobre, 2023). A growing body of literature has also highlighted the pragmatic nature of internal attention, demonstrating that it can proactively prioritise action-related contents in working memory (Boettcher et al., 2021; Formica et al., 2021; González-García et al., 2020; Henderson et al., 2022; Kikumoto et al., 2022; Nasrawi et al., 2023; Nasrawi & Van Ede, 2022; Rösner et al., 2022; Schneider et al., 2017; van Ede et al., 2019a). Sensory and action-related contents can co-exist in working memory. When an item in working memory is probed, the selection of its sensory- and motor-associated contents starts concurrently (van Ede et al., 2019a). However, there is much left to discover concerning the relationship of sensory- and action-related modulation in working memory.

Electroencephalography (EEG) provides a powerful method to independently track the prioritisation of sensory- and action-related contents in working memory. The selection of action plans is mirrored by a relative reduction in mu-beta (8-30 Hz) activity contralateral to the prospective hand action at central electrodes (e.g., Kaiser et al., 2001; Pfurtscheller et al., 2000; Schneider et al., 2017; van Ede et al., 2019a). In turn, the selection of stimulus locations in working memory is mirrored by a relative reduction in contralateral alpha-frequency (8-12 Hz) activity in posterior electrodes (e.g., Mok et al., 2016; Myers et al., 2014; Poch et al., 2014; Schneider et al., 2016; van Ede et al., 2017; Wallis et al., 2015). Moreover, small changes in gaze position become biased toward the prioritised locations in working memory (Liu et al., 2022; van Ede et al., 2019b, 2021).

It is becoming increasingly clear that the prioritisation of sensory contents in working memory is a highly dynamic and flexible process (De Vries et al., 2018; Lewis-Peacock et al., 2012; Myers et al., 2018; Rerko & Oberauer, 2013; van Ede et al., 2021; Van Moorselaar et al., 2015). For example, the prioritisation of sensory contents, as measured with EEG activity modulations and pupil size, changes according to temporal expectations concerning the likely time of an item to be probed (van Ede et al., 2017; Zokaei et al., 2019). However, it remains unknown whether the prioritisation of action-related contents can be similarly tuned to the temporal structure of the task. Additionally, while sensory- and action-related contents can be prioritised concurrently (van Ede et al., 2019a), it is unclear whether these two aspects of the representation are functionally bound. Does their prioritisation co-evolve in lockstep according to temporal expectations based on the dynamic structure of the task?

To address these questions, I designed a task that zoomed into how temporal expectations guide the dynamic prioritisation of sensory- and action-related contents that co-exist in working memory. Item location (left vs right side) was orthogonally crossed with required action (left vs right hand). The design thus enabled tracking the prioritisation of sensory contents (location) and prospective actions independently. Contralateral alpha (8-12 Hz) and mu-beta (8-30 Hz) attenuation provided markers of the prioritisation of sensory- and action-related contents in working memory, respectively. Gaze position provided an additional marker of location selection. To foreshadow the results, the prioritisation of both sensory- and action-related contents evolved flexibly as a function of dynamically changing expectations. However, their prioritisation was not temporally coupled, suggesting that multiple modulatory functions can operate in tandem on different aspects of working-memory representations.

4.2.2 Methods

4.2.2.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R57489/RE006). The sample size of the present study was based on previous studies investigating related questions (Boettcher et al., 2021; van Ede et al., 2019a). Thirty-one volunteers participated in two visits each. All participants self-reported having normal or corrected eyesight. They provided written consent before each visit and were reimbursed at £15/h for their participation.

Exclusion criteria were pre-defined. Participants were excluded from further analyses if their average performance error or RT was above 3 SDs from the mean error or RT, respectively, across all participants in either visit. Data from one participant were excluded from further analyses based on these criteria. The final sample (n = 30) had an average age of 23.57 (SD: 3.85). Three individuals were left-handed and twenty-seven were right-handed by self-report; six participants identified as male, twenty-three as female, and one as non-binary.

4.2.2.2 Experimental procedure and stimuli

I designed a visual-motor working-memory task to study the flexible and dynamic prioritisation of visual and action-related contents in working memory (**Figure 4.1a**). Participants were shown two coloured, tilted bars and were asked to report the tilt of one of the bars at the end of each trial. In half of the trials (*informative*), two key pieces of information allowed participants to anticipate which of the two items they would have to report: 1) a retro-cue matching the colour of one of the bars; and 2) the duration of the delay following the retro-cue and before the response probe. Participants reported the bar's orientation at the end of the trial. Importantly, the bar orientation (left vs right) was linked to the hand (left vs right) of the response. Additionally, the location of the bars (left vs right) and the direction of their tilt (left vs right) were manipulated orthogonally. Therefore, the prioritisation of bar locations and prospective hand actions could be tracked independently using their respective EEG and eye-tracking markers (see also Boettcher et al., 2021; van Ede et al., 2019a, 2019b).

The experimental script was generated using the Psychophysics Toolbox version 3.0.18 (Brainard, 1997) on Matlab 2022a (The Mathworks Inc., Natick, NA, USA).

Participants sat in a dimly lit room, ~60 cm away from a monitor (Dell U2312HM; 1920x1080 pixels resolution; 100-Hz refresh rate).

The background colour of the display was grey (#7F7F7F) for the duration of the task. At the beginning of each trial, participants saw the encoding display made of a white central fixation cross (#FFFFFF; 14 pixels) and two coloured, tilted bars shown for 250 ms. One bar was always on the left and the other on the right side of the screen. Each bar was centred 192 pixels (5.2 DVA) away from of the central fixation cross, had a length of 192 pixels and a width of 38 pixels. One bar was always tilted leftward and the other rightward. Bar tilts were drawn from one out of three possible bins with a uniform distribution of orientations (+/-10-33°, +/-34-57°, and +/-58-80°). To avoid cardinal effects, none of the displayed bars had orientations along the vertical or horizontal meridians. Orientation bins were counterbalanced such that all bins were equiprobably sampled for each participant. Bar location and tilt were orthogonally manipulated, such that leftward- and rightward-tilted bars were equally likely to appear on the left or right side of the screen across trials. The two bars on the encoding display had two different colours out of four possible, highly distinguishable colours: blue (#00DEFF), orange (#FFAC00), pink (#FF62FF), and green (#00ED82). Colours were counterbalanced across trials such that all possible combinations of colour, location, and tilt were displayed.

Following the encoding display, the coloured bars disappeared, and the central fixation cross remained on the screen for 750 ms (delay 1; **Figure 4.1a**). Subsequently, the colour of the central fixation cross changed for 200 ms (retro-cue). In half of the trials (*informative;* 50%), the colour of the retro-cue matched the colour of one of the two bars displayed previously. In the other half of the trials (*noninformative;* 50%), the fixation cross changed to a different colour that matched neither encoded item on that trial. The colour of the cue was chosen from the four possible colours detailed above. Cue colour was counterbalanced such that all colours acted as cues in the same number of trials across the task and appeared equiprobably in informative and noninformative trials.

In half of the informative and half of the noninformative trials, the response probe appeared 1 s after cue offset (*short* trials; 50%). In the other half of the trials, the response probe appeared 3 s after cue offset (*long* trials; 50%). During the post-cue delay (short and long), only a white, central fixation cross remained on the screen.

Crucially, in informative trials, two pieces of information predicted which of the two bars would be probed at the end of the trial with 100% validity: 1) the colour of the retro-cue; and 2) the duration of the delay between the cue and the probe. When the cue was informative (matching the colour of one of the two bars displayed at encoding) and the delay following the cue was short (1 s), participants were prompted to report the orientation of the cued bar at the end of the trial (100% validity). Alternatively, in informative trials with a long delay (3 s), participants were always required to report the orientation of the other (uncued) bar. Therefore, participants were encouraged to attend to the retro-cue and to track the duration of the subsequent delay to know which of the two bars they would be asked to report. In informative trials, they could anticipate reporting the item with the cued colour after the short interval. Once the short interval passed, they could shift the focus of attention to anticipate the item with the other colour. In noninformative trials, which of the two bars would be probed was unpredictable.

Following the delay, the colour of the central fixation cross changed again (probe) prompting participants to reproduce the tilt of the colour-matching bar (**Figure 4.1a**). To this end, participants used the "F" and "J" keys on the keyboard with their left and right index fingers respectively. Upon response initiation, a grey bar appeared centrally in the vertical position. Pressing the "F" key led to a counterclockwise rotation of the grey bar and pressing the "J" key made it move clockwise. Participants were instructed to release the key when the grey bar reached the desired orientation. The size of the grey bar was the same as that of the coloured bars on the encoding display. The grey bar did not rotate further than 90° in either direction. Therefore, leftward tilted bars could only be reported with the left hand and rightward tilted bars with the right hand. The response key could not be changed once a response was initiated. Participants were instructed to report the orientation as quickly and accurately as possible. They had a maximum of 3 s to respond from probe onset.

If participants responded with the correct key (F for leftward-tilted bars and J for rightward-tilted bars), they received visual feedback about the percentage accuracy of their response. If they pressed the incorrect key, they received the message “Wrong target!”. If they did not respond, they saw “Too slow!”. All feedback appeared centrally in white letters and was displayed for 500 ms. ITIs followed a beta distribution with a minimum of 3 s, maximum of 10 s, and average of 5.5 s. During each ITI, a white fixation cross was displayed centrally.

The present study was divided into two separate visits in which participants repeated the same task procedure. The first visit consisted of a behavioural session in which participants completed 8 blocks of 32 trials each for a total of ~1 h. The second visit consisted of an EEG and eye-tracking session in which participants completed 15 blocks with 32 trials each for a total of ~2.5 h. Every 5 blocks, participants had the chance to rest for 10-15 minutes. Before beginning the first session of the experiment, participants were walked through the instructions of the task and were asked to practice the procedure for at least one block.

4.2.2.3 Behavioural data analysis

Behavioural data were analysed using the R statistical programming language (version 4.2.1; R Core Team, 2021) and R studio (version RStudio 2022.07.1; RStudio Team, 2022). Report errors were calculated as the absolute difference between the reported orientation and the orientation of the probed bar. RT was defined as the time from probe onset until response initiation. Trials without a response, trials with RTs faster than 100 ms, trials with RTs slower than three times the SD of the average RT per participant, and trials with report errors higher than three times the SD of the participant-average error were excluded from further behavioural analyses. This resulted in an average removal of 2.82% (SD: 0.6%) of trials.

The statistical significance of the dependent variables of interest across participants (report error and RT) was tested using repeated-measures ANOVA with informativeness (informative and noninformative) and duration (short and long) as factors. The metric of effect size was η^2 and the within-subject SEM was quantified using the normalised data (Morey, 2008). Paired-samples Student's t-tests were used for post-hoc comparisons, and the effect size was reported as Cohen's d.

4.2.2.4 EEG: acquisition and preprocessing

EEG was acquired using a 64-channel Quik-Cap Neo Net cap (Ag/AgCl electrodes), Synamps amplifiers, and the CURRY 8 acquisition software (Compumedics Neuroscan). Sixty-four channels were distributed across the scalp following the international 10-10 positioning system. Data were referenced online to a reference channel positioned between Cz and CPz. Another channel (AFz) was used as the ground. Vertical and horizontal EOG were simultaneously recorded using a bipolar system integrated into the cap. Horizontal EOG electrodes were placed on the side of each eye and vertical EOG was positioned above and below the left eye. ECG was measured with an integrated, bipolar set-up. The upper ECG was placed on the left ribcage, centred above the left chest; the lower ECG was placed on the side of the left ribcage. During set-up, electrode impedance was lowered to below 5 kiloohms where possible and was at least below 10 kiloohms. Data were digitised at 1,000 Hz and filtered at 500 Hz during acquisition.

All EEG data were processed and analysed in Python 3.11 using MNE-Python (version 1.5.1; Gramfort, 2013) and custom-made scripts. First, data were notch-filtered at 50 Hz, and high-pass (0.05 Hz) and low-pass (40 Hz) filtered with a Finite Impulse Response (FIR) filter. Subsequently, the continuous data were visually inspected. Channels deemed "bad" were interpolated using spline interpolation as implemented with the *interpolate_bads* function in MNE-Python. Then, data were down-sampled to 250 Hz and re-referenced to the sensor average. An independent component analysis (ICA) identified artefacts related to eye movements by correlating individual ICs with the EOG signals. Based on the correlation values and visual inspection of IC time courses and topographies, ICs capturing eye-related activity were identified and subtracted from the EEG data. An average of 0.93 ICs (SD: 0.31; range: 0-2) were removed per participant.

Subsequently, the raw EEG data were epoched around cue onset and probe appearance (-0.25 s to 1.25 s in short trials and -0.25 s to 3.25 s in long trials) and activity during the baseline period (-0.25 to 0 s) was subtracted from each epoch. A surface Laplacian transform was applied to the epoched data using the *compute_current_source_density* MNE-Python function to reduce the effects of volume conduction and thus increase the spatial resolution and interpretability of the results.

In the EEG analyses, included trials were limited to those in which participants had pressed the correct key and RT was higher than 100 ms. Noisy trials, as identified on the epoched EEG time courses using a Generalized ESD procedure (Rosner, 1983), were also excluded. In total, 89.67% (SD: 5.34%) of trials were used in subsequent analyses.

4.2.2.5 EEG: time-frequency analyses

All EEG analyses focused on the period of interest from retro-cue onset until probe onset (**Figure 4.1a**). The retro-cue in informative trials was hypothesised to prompt participants to direct attention to the cued sensory (location) and action-related (response hand) contents in working memory. Importantly, it was hypothesised that in long trials, participants would "shift" to prioritising the other stimulus location and response hand after the short interval lapsed. Crucially, given the orthogonal manipulation of bar location and tilt, prioritisation of locations and action plans could be tracked independently with EEG (see also Boettcher et al., 2021; van Ede et al., 2019a). Specifically, it was hypothesised that EEG alpha-frequency activity (8-12 Hz) at occipital electrodes contralateral to the location of the prioritised item would be reduced. In parallel, it was predicted that EEG mu-beta activity (8-30 Hz) at central electrodes contralateral to the prioritised response hand would be reduced. Alpha-band activity (8-12 Hz) at left (PO7) and right (PO8) visual sensors was used to track sensory-related prioritisation. Mu-beta activity (8-30 Hz) in left (C3) and right (C4) motor electrodes was used to track action-related prioritisation (see also Boettcher et al., 2021; van Ede et al., 2019a). The same pattern of findings was confirmed using a larger cluster of lateralised visual and motor sensors (**Supplementary Figure 7.6**).

The epoched EEG time series were transformed into their time-frequency decompositions by convolving them with a 300-ms Morlet wavelet from 2 to 40 Hz in steps of 1 Hz. The 50 ms around the two edges of each epoch were subsequently cropped to remove any edge artefacts related to the time-frequency decomposition. Time-frequency activity in lateralised visual (PO7/PO8) and motor (C3/C4) channels was contrasted between trials in which either the stimulus location or the prospective action hand (related to the tilt), respectively, was contralateral vs ipsilateral to each channel. This was calculated and normalised as follows: [((contra – ipsi)/(contra + ipsi)) * 100], separately for left and right sensors per participant. Subsequently, the contrast across both sides was collapsed in the visual and motor selection conditions separately and averaged across participants. The time-frequency contrasts averaged across participants are shown in **Figure 4.2** (informative trials) and **Supplementary Figure 7.7** (noninformative trials). The average time-frequency activity in the early period (-0.2 to 1.2) includes both short and long trials. The later period (1.2 to 3.2) includes only long trials.

The same procedure was followed with each symmetrical electrode pair to create the topographical lateralisation maps shown in **Figure 4.2c**. The topographies show alpha and mu-beta left-versus-right contrasts across channels on the time points that correspond to the statistically significant clusters (see **Cluster-based permutation testing**).

Additionally, to generate the time course of posterior alpha and central mu-beta modulations, signals from the pre-defined frequencies were averaged at the selected channels. The time courses for the normalised change in posterior alpha (PO7/PO8;

8-12 Hz) and in central mu-beta (C3/C4; 8-30 Hz), are compared in **Figure 4.2c**. Additionally, the mu (8-12 Hz) and beta (14-30 Hz) bands were also averaged separately as shown in **Supplementary Figure 7.8**.

4.2.2.6 EEG: latency quantification

Next, the temporal relation between the time courses of the two frequency bands of interest (alpha and mu-beta) were investigated. A set of key control points was identified on the trial-average time courses following two approaches: 1) estimating the control points per participant and 2) using a hierarchical bootstrapping procedure (Saravanan et al., 2019).

In the first approach, the participant-average alpha and mu-beta time courses were smoothed using a Gaussian kernel with a SD of 12 ms to remove potential noise and facilitate the identification of the control points. For each participant, the minimum point of alpha and mu-beta attenuation was identified within a pre-defined time window (0.1 to 1 s from cue onset), and the maximum point of alpha and mu-beta was identified in a later window (1 to 2.5 s from cue onset). Subsequently, the time of zero crossing between the identified minimum and maximum was identified as the shift time. When participants had multiple zero crossings between the minimum and maximum time points, the earliest, average, and latest shift times were calculated. A two-sided paired-samples t-test compared the mean shift times of the alpha time course and the mu-beta time course (**Figure 4.3a**). The effect size was reported as Cohen's d.

In the hierarchical bootstrapping approach, half of the trials in half of the participants were randomly sampled over 100 iterations. For every sampled participant and subset of trials, the contralateral-versus-ipsilateral alpha and mu-beta time courses were calculated. The time courses were smoothed using a Gaussian kernel with a SD of 12 ms to facilitate the identification of the control points: the minimum and maximum alpha/mu-beta modulation times, the minimum shift time, the mean shift time, and the maximum shift time. Next, the mean shift times of the alpha and mu-beta time courses were compared across all iterations using a two-sided paired-samples t-test (**Figure 4.3b**). The effect size was reported with Cohen's d.

4.2.2.7 EEG: relation to behaviour

Subsequently, I investigated the relation between the two behavioural dependent variables of interest (report error and RT) and the modulation of alpha and mu-beta-frequency activity during the post-cue delay in informative trials separately for trials with a long and a short delay. For each participant and trial type (short and long), the median RT was estimated, and the trials were divided into those that were faster (fast) and those that were slower (slow) than the median RT. In parallel, the median report error was calculated. Trials were then separated into those with more (precise) or less accurate (imprecise) reports than the median error. Subsequently, I calculated the contralateral-versus-ipsilateral alpha and mu-beta contrasts in fast vs slow trials and in precise vs imprecise trials and compared them using cluster-based permutation testing as detailed below (**Figure 4.4**).

4.2.2.8 Eye-tracking data analyses

In visit 2 (EEG), bilateral eye position was continuously monitored with an eye-tracking device at a sampling rate of 1000 Hz (Eyelink 1000, SR-Research Ltd., Ottawa, Ontario, Canada). Participants performed an eye-tracking calibration task before blocks 1, 6, and 11 of the experiment. Additional calibration tasks were performed if ocular drift was noticed between these moments. Calibration did not work for three participants and eye-tracking data could not be collected. One participant was excluded who did not meet the behavioural inclusion criteria. Additionally, three other participants were excluded because the eye-tracking signal was lost for more than 50% of the trials. In total, eye-tracking data from 24 participants were analysed.

The eye-tracking signal was pre-processed following the steps detailed in related studies (e.g., Drachkow et al., 2022; Gresch et al., 2024; van Ede et al., 2019b). First, the acquired edf files were converted into the asc format using EDFConverter (SR-Research Ltd.). All subsequent analyses were performed using R studio (RStudio Team, 2020), the *eyelinker* R library, and custom-made scripts.

Eye-blinks were identified and the signal +/-100 ms around each blink was discarded following the guidelines from the Eyelink manual (Eyelink 1000, SR-Research Ltd., Ottawa, Ontario, Canada). Subsequently, data from the left and right eye were averaged yielding one time course for eye movements along the horizontal axis (x-position) and another along the vertical axis (y-position). In the present study, the bars were positioned along the horizontal axis. Therefore, only the horizontal gaze position was analysed further.

Next, data were epoched from 500 ms before to 3400 ms after cue onset in long trials and between -500 and 1400 ms in short trials. Trials with eye movements exceeding half the distance to the bars (96 pixels) were removed from further analyses (see also Gresch et al., 2024). Additionally, trials with RTs below 100 ms or with incorrect responses were discarded from further analyses. An average of 13.05% of trials (SD: 11.15%) were excluded.

The time course of the horizontal gaze position in each trial was smoothed with a 20-ms moving window. Subsequently, the epochs were cropped between 200 ms before and 1200 ms (short) or 3200 ms (long) after the cue to remove any smoothing-related edge artefacts. Finally, the average baseline activity (-200 to 0 ms), was subtracted from each epoch.

Leftward and rightward gaze-position time courses were compared between trials where the left or the right item was cued (**Figure 4.5a**). Additionally, "towardness" was calculated as the subtraction between the trial-average gaze position in trials where the right item was prioritised and the sign-flipped mean gaze position in left-item trials divided by two. Thus, towardness indicated the extent of biases in gaze position towards the prioritised item location. Statistical contrasts compared gaze position during leftward and rightward shifts and compared the towardness metric against zero using cluster-based permutation as described below.

4.2.2.9 Cluster-based permutation testing

Cluster-based permutation (Maris & Oostenveld, 2007) tested for statistical differences in the contralateral-versus-ipsilateral contrasts and eye-tracking time courses. This statistical approach assumes the effects of interest are clustered across the relevant dimensions (e.g., time, time-frequency, space-time-frequency), making it suitable for testing the statistical significance of time and time-frequency activity patterns in EEG and eye-tracking data.

First, a mass-univariate t-test (two-sided, alpha = .05) was performed on the group-level contralateral-versus-ipsilateral contrasts, and the sum of all t-values in a cluster was defined as the cluster statistic for each given cluster. Next, the time-frequency contralateral-versus-ipsilateral contrasts across the two conditions of interest (informative vs noninformative) were randomly permuted (sign-flipped) 10,000 times for each participant. The largest clusters found under this null hypothesis were compared with the cluster statistics in the observed data. For each cluster, the proportion of permutations whose largest cluster exceeded the cluster identified in the observed data was calculated and the resulting p-value was estimated. Importantly, this approach circumvents the common problem of multiple comparisons by comparing distributions of the summary cluster statistics. Cluster-based permutation was used on time-frequency spectra of the contralateral-versus-ipsilateral contrast in informative trials vs noninformative trials (null hypothesis). A similar procedure was used to compare the alpha, mu-beta, and gaze-position time courses against a null hypothesis of zero and against each other.

4.2.3 Results

The present study investigated whether and how sensory- and action-related working-memory contents could be prioritised as a function of dynamically evolving expectations.

4.2.3.1 Behavioural results

If participants prioritised each of the relevant working-memory contents at the expected times, their responses were hypothesised to be faster in both short and long informative trials as opposed to noninformative trials. Across both experimental visits (behavioural and EEG), repeated-measures ANOVAs of RT with informativeness and duration as factors revealed a main effect of informativeness on RT (*visit 1*: $F(1,29) = 130.47$, $***p < .001$, $\eta^2 = .25$; *visit 2*: $F(1,29) = 188.42$, $***p < .001$, $\eta^2 = .26$), a main effect of duration on RT (*visit 1*: $F(1,29) = 73.6$, $***p < .001$, $\eta^2 = .09$; *visit 2*: $F(1,29) = 78.71$, $***p < .001$, $\eta^2 = .07$), and no interaction between the factors (*visit 1*: $F(1,29) = 1.98$, $p = .17$, $\eta^2 = .002$; *visit 2*: $F(1,29) = .11$, $p = .74$, $\eta^2 < .000$; **Figures 4.1b** and **4.1d**). Overall, participants were faster at responding to targets in informative trials than noninformative, thus suggesting that retro-cues and internally driven temporal expectations facilitated performance in this task. Moreover, participants were faster in long trials compared to short trials.

Report errors in the task were consistently low and insensitive to the informativeness of the retro-cue on either visit (*visit 1*: $F(1,29) = .45$, $p = .5$, $\eta^2 < .001$; *visit 2*: $F(1,29) = .23$, $p = .63$, $\eta^2 < .001$). A main effect of duration on error indicated smaller errors (higher accuracy) on short trials than long trials (*visit 1*: $F(1,29) = 4.3$, $*p = .02$, $\eta^2 = .005$; *visit 2*: $F(1,29) = 20.72$, $***p < .001$, $\eta^2 = .03$). The factors did not interact (*visit 1*: $F(1,29) = 1.64$, $p = .2$, $\eta^2 = .002$; *visit 2*: $F(1,29) = 1.49$, $p = .23$, $\eta^2 = .001$; **Figure 4.1c** and **4.1d**).

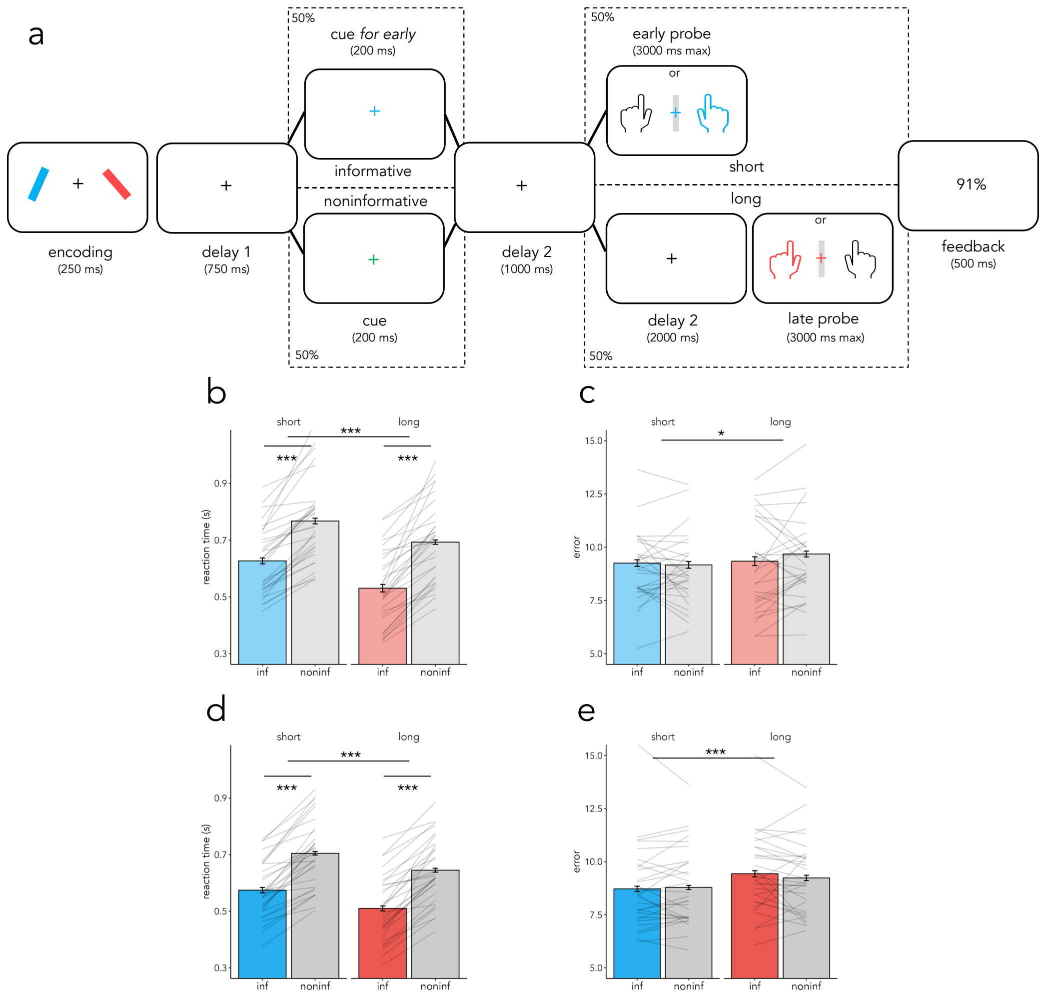


Figure 4.1. Visual experiment: task design and behavioural results. a) Trial schematic. Two coloured, tilted bars (one on the left and the other on the right; one tilted to the left and the other to the right with location and tilt being orthogonally manipulated) were displayed at encoding. In half of the trials (informative) a retro-cue matching the colour of one of the two bars was shown and in noninformative trials (50%) a cue with a distinct colour appeared instead. In informative trials, if the delay after cue offset was short (1 s), participants were probed about the cued item. Alternatively, if the delay was long (3 s), they had to report the other (uncued) item. In noninformative trials, the probed item was unpredictable. Reaction time (s) (panel b) and report error (°) (panel c), in informative and noninformative and short and long trials in visit 1 (behavioural session). *RT (s)*: $M_{inf/short}$: .63, $SD_{inf/short}$: .06, $M_{noninf/short}$: .77, $SD_{noninf/short}$: .06, $M_{inf/long}$: .53, $SD_{inf/long}$: .07, $M_{noninf/long}$: .69, $SD_{noninf/long}$: .04; *Error (°):* $M_{inf/short}$: 9.25, $SD_{inf/short}$: .85, $M_{noninf/short}$: 9.17, $SD_{noninf/short}$: .86, $M_{inf/long}$: 9.34, $SD_{inf/long}$: 1.13, $M_{noninf/long}$: 9.68, $SD_{noninf/long}$: .76. Reaction time (s) (panel d) and report error (°) (panel e), in informative and noninformative and short and long trials in visit 2 (EEG session). *RT (s)*: $M_{inf/short}$: .57, $SD_{inf/short}$: .05, $M_{noninf/short}$: .7, $SD_{noninf/short}$: .04, $M_{inf/long}$: .51, $SD_{inf/long}$: .05, $M_{noninf/long}$: .65, $SD_{noninf/long}$: .04; *Error (°):* $M_{inf/short}$: 8.72, $SD_{inf/short}$: .68, $M_{noninf/short}$: 8.79, $SD_{noninf/short}$: .54, $M_{inf/long}$: 9.43, $SD_{inf/long}$: .79,

$M_{noninf/long}$: 9.24, $SD_{noninf/long}$: .7. Thin grey lines represent individual participants, error bars represent the SEM, grey represents noninformative trials and colours depict informative trials (red: short, blue: long). More transparent colours reflect visit 1 and less transparent colours visit 2.

4.2.3.2 EEG: alpha- and mu-beta-frequency activity modulation

Next, I turned to the pre-defined alpha- and mu-beta-frequency EEG activity during the post-cue delay. Based on previous studies (e.g., van Ede et al., 2019a), alpha activity contralateral to the selected item location was hypothesised to be modulated by the internal prioritisation of locations. Additionally, mu-beta activity contralateral to the prospective action hand was predicted to change together with prospective action selection. Cluster-based permutation analyses of the time-frequency spectra in the ipsilateral-versus-contralateral contrasts of visual and motor selection in informative trials vs the same contrast in noninformative trials confirmed these hypotheses (see **Supplementary Figure 7.7**).

A pronounced reduction in alpha activity contralateral to the selected item location was observed following the retro-cue in the early part of the post-cue period which contained both short and long trials (**Figure 4.2a**; first cluster: $***p < .001$). Strikingly, in long trials, the side of relative alpha attenuation shifted as the interval exceeded that for probing at the short time (**Figure 4.2a**; second cluster: $*p = .04$). This "shift" in alpha activity from one hemisphere to the other was suggestive of a sequential prioritisation of the cued item location first and the un-cued item location later (**Figure 4.2c** in burgundy; first cluster: $***p < .001$; second cluster: $*p = .03$).

In parallel, a noticeable early reduction in mu-beta activity occurred in contralateral motor areas with respect to the response hand signalled by the retro-cue in both short and long trials (**Figure 4.2b**; first cluster: $**p = .002$). Strikingly, the side of mu-beta attenuation also shifted from one hemisphere to the opposite, mirroring the flexible prioritisation of successive action plans corresponding to the first and second items, respectively (**Figure 4.2b**; only long trials; second cluster: $***p < .001$).

These findings were confirmed on the average time course of mu-beta activity (**Figure 4.2c** in green; first cluster: $^{**}p = .003$; second cluster: $^{***}p < .001$). Importantly, the present findings were not dependent upon EEG sensor choice. Selection of a larger set of visual and motor channels revealed an equivalent pattern of results (**Supplementary Figure 7.6**).

Similar to previous studies (e.g., van Ede et al., 2019a), the modulation of alpha activity linked to the prioritisation of item location had a lateralised occipital (visual) EEG topography. Alternatively, changes in mu-beta activity were predominantly confined to central (motor) EEG channels (**Figure 4.2c**). The prioritisation of the first and second location both modulated alpha-frequency activity with comparable topographies. Similarly, the prioritisation of the first and second prospective actions had similar topographies and modulated the same mu-beta frequency band.

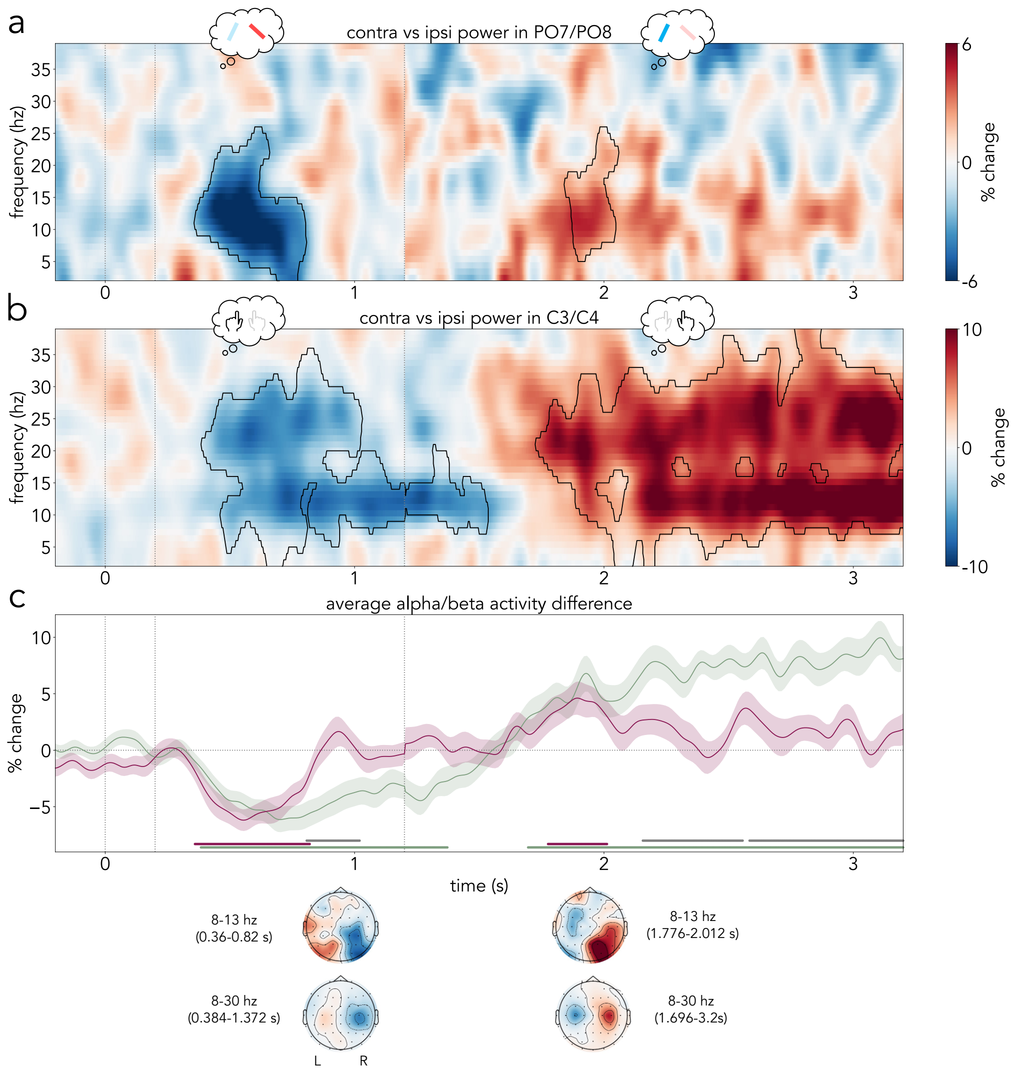


Figure 4.2. Visual experiment: frequency-specific EEG activity locked to cue onset in informative trials. a) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued bar location in occipital sensors (PO7/PO8) divided by summed contralateral and ipsilateral activity and expressed as a percentage. b) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued prospective action in central sensors (C3/C4) divided by summed contralateral and ipsilateral activity and expressed as a percentage. c) Average alpha (8-12 Hz) activity difference between contralateral and ipsilateral sensors to the cued location across participants (burgundy) and average mu-beta (8-30 Hz) activity between contralateral and ipsilateral sensors to the cued action across participants (green). Black outline indicates significant clusters. Shaded areas represent the SEM and cluster-permutation corrected significant time points are indicated with horizontal lines (burgundy: alpha vs null; green: mu-beta vs null; grey: alpha vs mu-beta). Topographies represent the average frequency-specific activity in left-versus-right contrasts across all sensors during the specified time-windows which correspond to the alpha and mu-beta clusters in panels a and b. The first part of the

time-frequency spectra in panels a and b and of the time course in c (-0.2-1.2 s) corresponds to the average of short and long trials, and the second part (1.2-3.2 s) corresponds to long trials only. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the retro-cue and the time of probe appearance in early trials (1.2 s).

Interestingly, visual inspection of the time-frequency spectra in **Figure 4.2b** suggested potential differences in the time courses of the lower mu-frequency band (8-13 Hz) and the higher beta activity (14-30 Hz) when shifting from one prospective action to the next (**Figure 4.2b**). Indeed, averaging across the mu and beta frequency bands separately revealed that mu activity was attenuated in the hemisphere contralateral to the prospective response hand until well after the time of early probe appearance, while, on average, the beta modulation returned to baseline earlier (**Supplementary Figure 7.8**).

Strikingly, the time courses of stimulus location and prospective hand action prioritisation seemed to follow distinct trajectories. Specifically, the prioritisation of location information was relatively short-lived in both selection events. Conversely, the prioritisation of the first and second prospective hand actions seemed to be longer-lasting. This observation was supported by the presence of statistically significant differences between the alpha and mu-beta time courses across the post-cue delay (first cluster: $^{*}p = .04$; second cluster: $^{**}p = .006$; third cluster: $^{***}p < .001$; **Figure 4.2c**).

These differences may suggest that, even when sensory and action-related contents co-exist in working memory, they can be selected at different times. Their prioritisation, therefore, need not be continuously coupled in time. To test the temporal coupling between the two signals, the average time at which the alpha (visual) and mu-beta (motor) time series crossed the y-axis per participant was compared. A paired-samples t-test between the average *shift time* across participants revealed that the *visual shift*, quantified on the alpha time series, occurred significantly earlier than the *motor shift*, quantified on the mu-beta time series ($t(29) = 4.3$, $^{***}p < .001$, $d = .87$; **Figure 4.3a**). The findings were confirmed using a hierarchical bootstrapping procedure, which revealed that the average shift time was consistently earlier for the *visual shift* than the *motor shift* ($t(99) = 19.5$, $^{***}p < .001$, $d = .78$; **Figure 4.3b**).

Interestingly, the average of the estimated *visual shift time* coincided approximately with the time of probe appearance in early trials. The *motor shift time* occurred around 300 ms later (participant-average mean: 305.1 ms; bootstrapping mean: 294.28 ms).

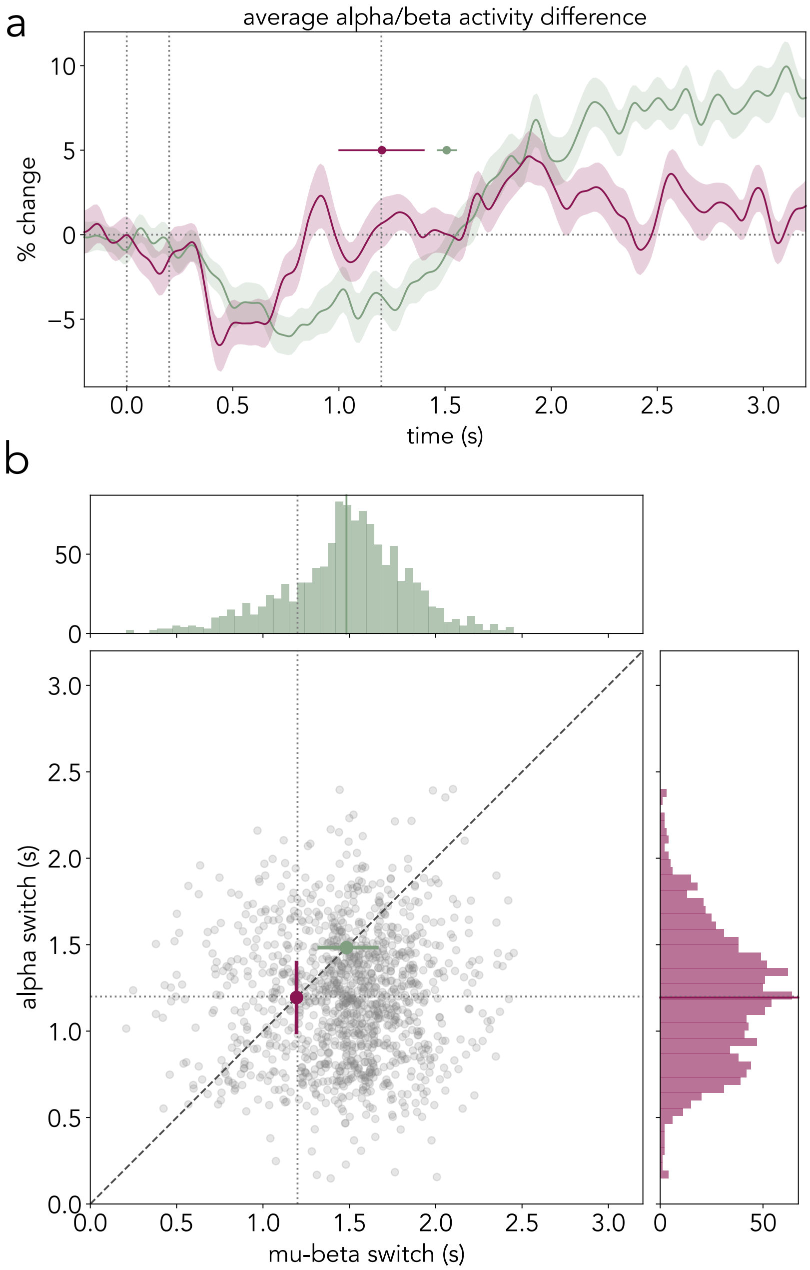


Figure 4.3. Visual experiment: average shift times of the alpha and mu-beta time courses. a) Average alpha (8-12 Hz) activity difference between contralateral and ipsilateral sensors to the cued location (burgundy) in long trials and average mu-beta (8-30 Hz) activity between contralateral and

ipsilateral sensors to the cued action (green) in long trials. Shaded areas represent the SEM. The burgundy circle represents the participant-average shift time as estimated on the alpha time course, and the green circle represents the shift time estimated on the mu-beta activity average. The edge of the line on the left of each circle represents the average minimum shift time across participants for the alpha and mu-beta time courses respectively. The edge of the line on the right of each circle depicts the average maximum shift time across participants. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the retro-cue and the time of probe appearance in early trials (1.2 s). b) Top and right: the histograms represent the distribution of average mu-beta (green) and alpha (burgundy) shift times, respectively, on the 100 iterations of the bootstrapping procedure (50 bins per histogram). Centre: scatter plot of the average mu-beta and alpha shift times in each of the 100 bootstrapping iterations (grey dots) as plotted on the mu-beta (x-axis) and alpha (y-axis) time space. Vertical and horizontal dotted lines represent the time of early probe appearance (1.2 s after retro-cue onset). The burgundy circle represents the participant-average shift time as estimated on the alpha time course, and the green circle represents the shift time estimated on the mu-beta activity average. The lines on each side of each circle depict the SEM across all bootstrapping iterations.

4.2.3.3 EEG: correlation with behaviour

Next, the relation between the behavioural variables of interest (report error and RT) and the alpha- and mu-beta-frequency activity patterns were investigated. Correlations with behavioural performance were observed for mu-beta modulations. Long informative trials with faster responses also displayed stronger suppression of mu-beta-frequency activity in the hemisphere contralateral to the hand of the second prospective action (first cluster: *$p = .02$; second cluster: **$p = .002$; third cluster: ***$p < .001$; **Figure 4.4b**). Interestingly, despite not showing a general effect of informativeness on report error (**Figure 4.1c** and **4.1e**), smaller errors (higher precision) in informative long trials were also related to a stronger mu-beta modulation (cluster: *$p = .02$; **Figure 4.4d**). Together, these results suggested that modulations in mu-beta activity were tightly related to performance. Alternatively, no significant clusters in lateralised alpha activity were found in fast vs slow trials nor precise vs imprecise trials (**Figure 4.4a,c**). Furthermore, first part of the post-cue delay showed no differences in the relation between behaviour and frequency-specific activity modulation.

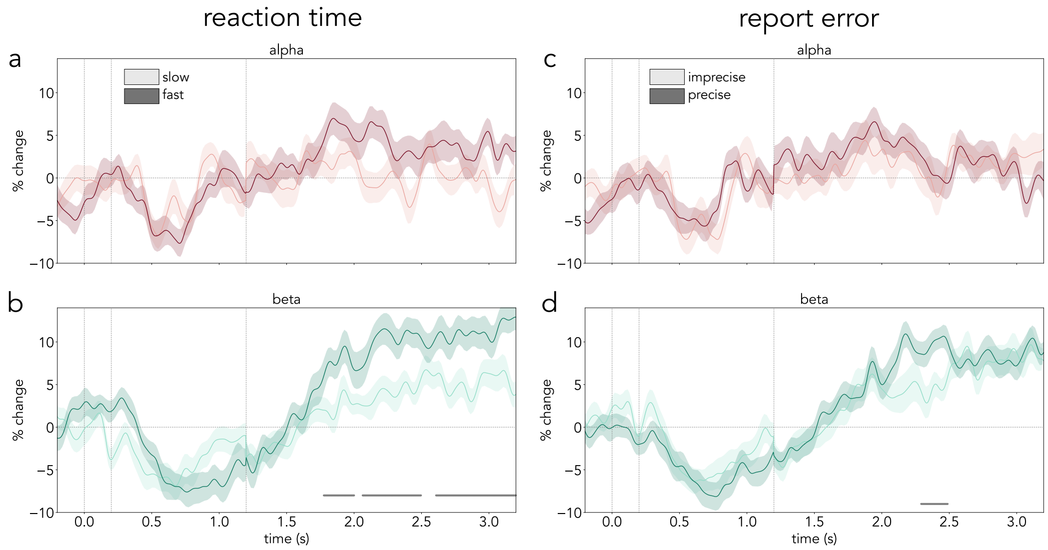


Figure 4.4. Visual experiment: correlation with behaviour. Alpha and mu-beta activity contralateral vs ipsilateral to the cued location/hand in fast vs slow and precise vs imprecise trials. a,b) Average alpha (8-12 Hz; pink/red) and mu-beta (8-30 Hz; light and dark green) activity difference between contralateral and ipsilateral sensors to the cued location/action in trials categorised as fast (dark) or slow (light) based on a median split of RT per participant. c,d) Average alpha (8-12 Hz; pink/red) and mu-beta (8-30 Hz; light and dark green) activity difference between contralateral and ipsilateral sensors to the cued location/action in trials categorised as precise (dark) or imprecise (light) based on a median split of report error per participant. Darker colours represent better (faster or more precise) performance. The first part of the time courses corresponds to the average of short trials only and the second part (1.2-3.2 s) corresponds to long trials only. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the retro-cue and the time of probe appearance in early trials (1.2 s). Cluster-based permutation significant time points of the contrast between the displayed time courses are indicated with horizontal grey lines.

4.2.3.4 Eye-tracking results

In addition to an attenuation of contralateral alpha activity over occipital EEG channels, the prioritisation of stimulus locations in visual working memory has also been shown to lead to small biases in gaze position in the direction of internally selected items (e.g., Liu et al., 2022; van Ede et al., 2019b, 2021). In the present study, shifting from prioritising one item location to the other was hypothesised to be accompanied by a shift in the direction of this gaze bias. Using the eye-tracking signal recorded in the second visit of the study (EEG session), the average horizontal gaze position locked to the retro-cue onset was estimated as a function of which location was cued (**Figure 4.5**). This revealed a significant bias of gaze position towards the location of the cued item first (**Figure 4.5a**; cluster: *p = .03; **Figure 4.5b** cluster: *p = .02), followed by a general bias of gaze towards the opposite location in long trials (**Figure 4.5a;** cluster: **p = .002; **Figure 4.5b**; cluster: **p = .002).

From this, it was concluded that the prioritisation of item locations in working memory as a function of dynamically evolving expectations was mirrored by biases in horizontal gaze position which were tuned to the relevant times.

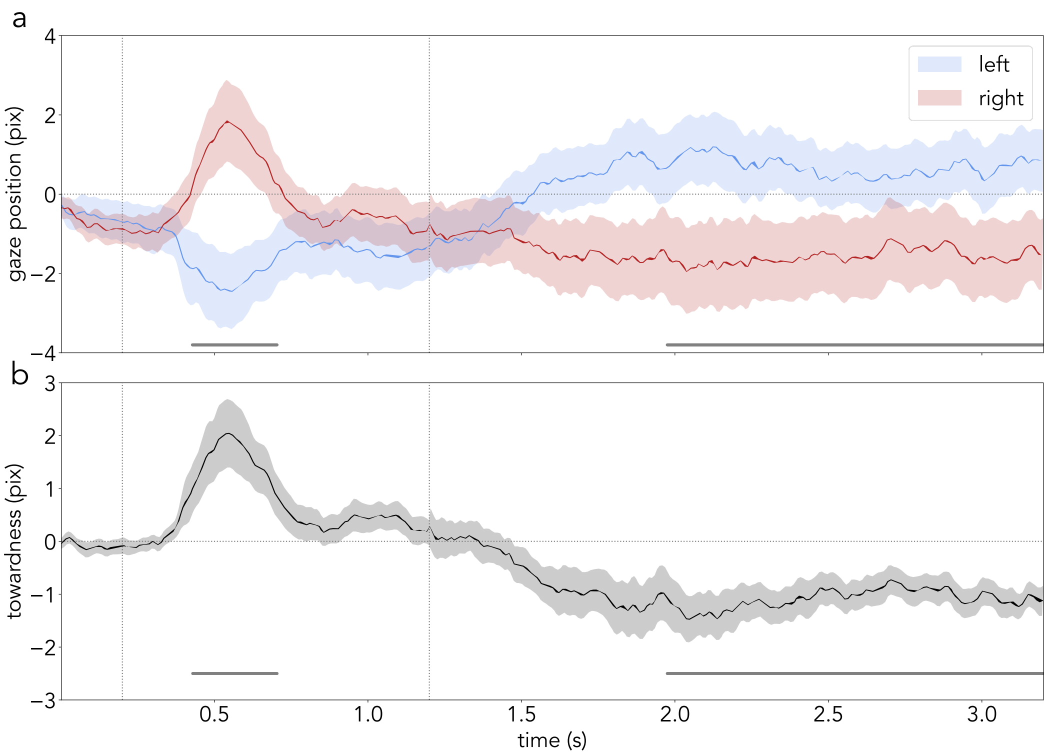


Figure 4.5. Visual experiment: horizontal gaze position as a function of cued item location locked to retro-cue onset in informative trials. a) Participant-average horizontal gaze position (in pixels) when an item on the left (blue) vs on the right (red) was cued locked to cue onset in informative trials. b) Participant-average towardness (metric which collapses across left and right cued items) locked to cue onset in informative trials. Shaded areas represent the SEM, and vertical dotted lines represent (from left to right) the offset of the retro-cue and the time of probe appearance in early trials. Cluster-permutation significant time points are indicated with horizontal grey lines. The first part of the time

courses (0-1.2 s) is the average across both short and long trials, and the second part (1.2-3.2) averages across long trials only.

4.2.4 Discussion

The present study reveals that both sensory and motor-related contents in working memory are dynamically and flexibly modulated in a temporally structured fashion as expectations develop and shift about the likely stimulus location and prospective response hand. Across two sessions, response times revealed that participants were faster when responding to targets at the expected times. Mirroring the behavioural results, alpha and mu-beta modulation time courses uncovered that the prioritisation of both sensory- and action-related contents in working memory was flexible (i.e., it "shifted" from prioritising the first to the second item/action) and temporally tuned (i.e., both instances of selection of the relevant item/action were temporally specific). Interestingly, however, the time courses of visual and motor prioritisation as measured with alpha and mu-beta EEG activity were not continuously coupled. In addition to modulations in EEG activity, gaze biases reflecting oculomotor readouts of the internal orienting of attention were also dynamically and flexibly modulated.

The present task successfully elicited a flexible and dynamic prioritisation of sensory and action-related working-memory contents, as indexed by multiple behavioural and physiological metrics. In contrast to most previous studies in which location and action selection were locked to the encoding display or the response probe (e.g., Boettcher et al., 2021; Nasrawi et al., 2023; van Ede et al., 2019a), here, the first location and action selection were driven by a retro-cue. Therefore, encoding of item colours, locations, orientations, and associated hand-actions was equivalent in this task (see also Ester & Weese, 2023; Schneider et al., 2017). Additionally, the delay between the retro-cue and the probe permits zooming into the behavioural and neural changes driven by anticipatory processes, and relatively isolated from the potential effects of an imminent response. Importantly, the orthogonal manipulation of item location and prospective hand action allowed for independent tracking of visual and motor prioritisation in working memory (see also van Ede et al., 2019a). Moreover, the present task could probe the interrelations between physiological signals such as EEG frequency-specific activity modulations and eye-tracking, and the complementary behavioural variables of interest, such as RT and report error.

Importantly, in this task, attentional shifts to other stimulus locations and associated actions were driven internally by temporal expectations. This manipulation is a good model for the signals that guide internal attention in typical dynamic contexts. Changes in task goals as a function of time are often internally driven, variable processes. Building on these key features, the present study replicates the finding that sensory content prioritisation in working memory is flexible (De Vries et al., 2017, 2018; LaRocque et al., 2013; Lewis-Peacock et al., 2012; Murray et al., 2013; Myers et al., 2018; Rerko & Oberauer, 2013; Van Moorselaar et al., 2015), dynamic, and temporally tuned (van Ede et al., 2017; Zokaei et al., 2019).

To the best of my knowledge, the present study is the first to reveal the flexible, dynamic, and temporally tuned nature of action-related content prioritisation in working memory. Specifically, action-related contents which were deprioritised in the first instance could be re-prioritised later as indexed by a strong mu-beta modulation and behavioural benefits in long trials. Importantly, the extent of mu-beta modulation correlated with enhanced task performance. Moreover, this study shows that action-related contents can be prioritised based on both external cues and internal states. The present study also lends support to the view that internal attention can prioritise not only immediately upcoming, specific actions, but also multiple, potential and prospective actions (see also Cisek, 2007; Cisek & Kalaska, 2010; Gallivan et al., 2015, 2016; Nasrawi et al., 2023; Nasrawi & Van Ede, 2022; Tanji, 2001). Here, the prioritisation of two distinct actions unfolded serially as a function of changing relevance.

The present task reveals that sensory and action-related contents that co-exist in working memory are both flexibly and dynamically prioritised. In external attention, temporal expectations have been reported to modulate different systems according to the goals of the task. Specifically, van Ede and colleagues (2020) showed that temporal expectations modulated spatial-sensory systems when the purpose of the task was perceptual and motor systems when speeded responses were emphasised. Complementing and extending these findings, the present study uncovered that temporal expectations could modulate different systems (sensory and motor) within the same task.

Interestingly, the modulation of sensory and motor contents follows a similar pattern when driven by an external cue or an internal state. Namely, the first and second instances of location prioritisation attenuated contralateral alpha activity with a seemingly comparable topography. Similarly, prioritising hand actions based on external cues or internal states influenced mu-beta activity over apparently similar contralateral central sensors. Nevertheless, the present study may have overlooked nuanced differences between cue- and internally driven selection, which could be further investigated in the future.

A central finding of the current study is that modulation of sensory and motor contents in working memory followed a similar pattern but were not strictly functionally coupled. The prioritisation of sensory- and action-related contents did not unfold in lockstep. Consistent with previous studies, modulation of alpha activity pointed to a transient selection of item locations (see also De Vries et al., 2017, 2018; Mok et al., 2016; Schneider et al., 2015, 2016). In contrast, mu-beta activity showed a longer-lasting modulation of motor systems. This is in line with the requirement to respond using the selected effector (left or right hand) at the end of the trial. Nevertheless, previous studies have found that preparatory mu-beta modulations can emerge, disappear during an interrupter task, and reemerge later (Boettcher et al., 2021). This suggests that the sustained motor modulation observed in the delay period of the present study may not be strictly necessary for successful task performance.

Relatedly, in long trials, mu-beta modulation persisted well into the second part of the delay, after the time of early probe appearance had passed. Probing (van Ede et al., 2019a) or cueing (present study; see also Ester & Weese, 2023) sensory- and action-related contents has been shown to trigger a parallel selection of both. Instead, the present task suggests that shifting between visual items and between motor contents based on internally driven temporal expectations decouples their time courses. Specifically, the present findings point to a systematic lag in the prioritisation of prospective hand actions compared to item locations.

Several interpretations could explain this finding, but further research will be necessary to arbitrate between them. For example, the relatively long duration of the second delay (2 s) may prolong the selection of the first action. Lingering selection and preparation of the first action does not compromise performance in long trials, since there is ample time to re-prioritise the second action. This intriguing possibility could be investigated by manipulating the duration of the delay in long trials. Alternatively, or additionally, temporal uncertainty may have different effects in different systems (visual and motor). This possibility can also be tested by systematically varying delays in both short and long trials.

The earlier and transient nature of the alpha modulation vs the later and longer-lasting changes in mu-beta activity are congruent with other studies which have suggested that working-memory contents may undergo a change from a sensory to a motor code as the requirement to respond takes precedence in the task (González-García et al., 2020; Henderson et al., 2022; Kikumoto et al., 2022; Panichello & Buschman, 2021). By zooming into the period of internal prioritisation, the present design shows how relevant sensory/action contents are prioritised as a function of when and for how long they are useful and relevant. The short-lived nature of alpha modulations and the earlier alpha shift time could reflect the fact that spatial orienting may help activate working-memory contents into a prioritised state (Stokes, 2015). Following this initial spatial selection, sustained spatial focus may no longer be useful or necessary, giving way to processes related to output gating and motor selection (see also (Myers et al., 2017; Wallis et al., 2015). Nevertheless, this and other studies have also shown that spatial and motor contents can be prioritised simultaneously and in parallel (van Ede et al., 2019a), suggesting that prioritisation of sensory and action-related contents is not always serial.

Interestingly, visual inspection of the time-frequency spectra in **Figure 4.2** revealed a difference in the prioritisation time courses of mu (8-12 Hz) and beta (13-30 Hz) activity, which was later confirmed statistically (**Supplementary Figure 7.8**). Mu and beta rhythms have been suggested to have distinct anatomical origins and to reflect the engagement of different brain networks (Ronnqvist et al., 2013; Salmelin et al., 1995; Salmelin & Hari, 1994). Consistent with their functional differences, the present findings show a temporal decoupling between both signals which coincides with the time of the early probe. This opens interesting avenues to explore the differential role of mu and beta rhythms in mediating the dynamic prioritisation of action plans in working memory.

Recently, physiological signals recorded from peripheral sources (e.g., the eye) have been shown to reflect changes in internal attention. Specifically, small shifts in gaze position towards the location of working-memory items follow the deployment of covert internal attention to specific locations (Liu et al., 2022; van Ede et al., 2019b). Here, I additionally discovered that biases in gaze position mirror the dynamic prioritisation of locations based on changing temporal expectations (see also van Ede et al., 2017). The result complements findings from a different study in which pupil size dynamically tracked the prioritisation of stimuli with different luminance contrasts in working memory (Zokaei et al., 2019). Together, this reinforces the utility of oculomotor proxies of internal shifts of attention.

This study found a consistent speeding of responses to expected items following both external cues and internally driven temporal expectations. Moreover, reaction times were smaller in informative and noninformative long trials vs short trials which may reflect increased preparedness to respond following a longer delay (e.g., Los, 2010). While no effects of informativeness were identified on report error, longer trials had higher errors in both informative and noninformative conditions, possibly due to a time-related decay in working-memory contents (Baddeley, 1986) or because of a speed-accuracy trade-off. Interestingly, despite a lack of an effect of informativeness on report error, mu-beta-frequency (proxy of motor selection) activity during the second part of the memory delay was stronger in precise than imprecise trials.

Additionally, mu-beta modulation was enhanced in faster trials as opposed to slower ones. Despite a modulation in alpha-frequency activity during the memory delay, the latter was not systematically correlated with behaviour. The relation between mu-beta modulation and behaviour was only statistically significant during the latter part of the post-cue delay, during which one certain prospective action was held in working memory. This poses questions about whether certain and immediate prospective actions modulate mu-beta activity differently from uncertain actions (but see Nasrawi et al., 2023; Nasrawi & Van Ede, 2022). Additionally, these findings point to a key role for mu-beta activity in flexibly prioritising motor contents in working memory and highlight its value as a functionally relevant marker of internal attention.

In the current task, the two bars were arranged spatially but their location was not strictly necessary for the task. Remembering the colour of the bars was sufficient to successfully use the coloured retro-cue and probe, and remembering their tilt was enough to select the correct response. Despite not being necessary, location was selected following the retro-cue and, interestingly, it was also re-prioritised when participants selected the second item on the basis of internally driven temporal expectations, as evidenced by the modulation in alpha activity in the second memory delay. This is consistent with other studies showing that spatial arrangement is stored in working memory even when it is task-irrelevant (e.g., Kuo et al., 2009; Sligte et al., 2008; Sreenivasan et al., 2014). A complementary question that remains unanswered is when other relevant object features were prioritised during the task (e.g., colour and orientation; Ester & Weese, 2023).

In summary, the present study shows that sensory and action-related contents that co-exist in working memory are flexibly and dynamically prioritised and tuned to the moments when they will become relevant. This points to a fine temporal organisation of internal attention according to external temporal regularities. Moreover, the prioritisation of sensory and action-related contents that co-exist in working memory was not found to be continuously temporally coupled. This speaks to the multiplicity of flexible and dynamic modulatory processes that co-occur to prepare internal representations for adaptive behaviour.

4.3 EXPERIMENT 2: AUDITORY

4.3.1 Introduction

Internal attention is the process of prioritising selective contents within internal representations to proactively guide behaviour according to goals, expectations, and other control functions (Heuer et al., 2020; Myers et al., 2017; Souza & Oberauer, 2016; van Ede & Nobre, 2023). In the laboratory, retro-cues are often used to orient attention to working-memory contents (Griffin & Nobre, 2003). In these tasks, participants encode a set of attributes into working memory and an informative cue during the working-memory delay (retro-cue) orients attention towards one of the encoded attributes. Informative retro-cues result in more accurate and faster reporting of attributes of the cued items (Astle et al., 2012; Griffin & Nobre, 2003; Landman et al., 2003; Sligte et al., 2010).

Internal attention can flexibly prioritise, de-prioritise, and re-prioritise visual contents in working memory (Christophel et al., 2018; De Vries et al., 2017, 2018; LaRocque et al., 2013; Lewis-Peacock et al., 2012; Muhle-Karbe et al., 2021; Myers et al., 2018; Rerko & Oberauer, 2013; van Ede et al., 2021). For example, selecting one item in working memory does not diminish the ability to select other encoded items later (Murray et al., 2013; Myers et al., 2018). Additionally, internal prioritisation is tuned to the moments when visual items are expected to become relevant (van Ede et al., 2017; Zokaei et al., 2019).

Auditory studies have similarly revealed retro-cueing benefits for reporting contents in auditory working memory (Backer et al., 2015, 2020; Backer & Alain, 2012; Fan et al., 2021; Lim et al., 2015). However, the extent to which auditory internal attention is flexible, dynamic, and temporally tuned is yet to be explored.

Cueing participants to attend to an external location or a location in working memory activates an overlapping network of frontoparietal areas, including key regions of the oculomotor system (Nobre et al., 2004; see also Bledowski et al., 2009; Esterman et al., 2009; Nee & Jonides, 2008; Tamber-Rosenau et al., 2011; Wallis et al., 2015). Moreover, visual contents in working memory are spatiotopically arranged even when space is not directly relevant to the task (e.g., Kuo et al., 2009, 2014; Schneegans & Bays, 2017; Sligte et al., 2008, 2010; van Ede et al., 2019a). Interestingly, oculomotor metrics of gaze position, microsaccades, and pupil dilation can track the prioritisation of visual items in working memory (van Ede et al., 2019b, 2021; Zokaei et al., 2019; see also Spivey & Geng, 2001). Accordingly, internal visual attention has been proposed to engage the oculomotor system and its peripheral effector organs, as in external visual attention (Deubel & Schneider, 1996).

Auditory and visual external attention engage partially overlapping and partially differing frontoparietal brain networks (Lee et al., 2014; Noyce et al., 2017; Spence & Santangelo, 2010; Zatorre et al., 1999). When auditory attention is directed to spatial locations, it has been suggested to build on brain systems that are typically dedicated to visual (spatial) attention (Lee et al., 2012; Michalka et al., 2015, 2016). However, less is known about the role of the oculomotor system in internal auditory attention. Interestingly, directing internal attention to the serial order of auditory (verbal) contents results in small shifts in gaze position (Sahan et al., 2022). This suggests that the internal prioritisation of auditory (verbal) working-memory contents can engage the oculomotor system. Nevertheless, it remains unclear whether prioritising sound locations in working memory can dynamically bias gaze position towards the prioritised locations.

In this study, the task introduced in Experiment 1 was adapted to investigate whether auditory contents in working memory could be flexibly and dynamically prioritised as a function of temporally evolving probabilities of different sounds being probed. Additionally, I tested whether biases in horizontal and vertical gaze position, as measured with eye tracking, dynamically tracked the prioritisation of sound location and pitch in auditory working memory. To foreshadow the results, participants could flexibly and dynamically prioritise contents in auditory working memory. Nevertheless, no modulations of gaze position were found as a function of the internal prioritisation of sound location and pitch.

4.3.2 Methods

4.3.2.1 Participants

This study was approved by the Central University Research Ethics Committee of the University of Oxford (R57489/RE006). The sample size of the present study was based on Experiment 1. Data from 30 participants were collected. All participants self-reported having normal or corrected eyesight and normal audition. They provided written consent before participation and were reimbursed at £15/h for their participation.

Based on pre-defined exclusion criteria, participants were excluded from further analyses if their average side accuracy (see **Behavioural data analysis** for details) on the task was below 60% or if their RT was above 3 SDs from the cross-participant mean RT. Data from six participants were excluded from further analyses based on these criteria. The final sample (n = 24) had an average age of 22.25 (SD: 4.97). Four individuals were left-handed and twenty were right-handed by self-report; five participants identified as male, eighteen as female, and one as non-binary.

4.3.2.2 Experimental procedure and stimuli

Based on the visual-motor task in Experiment 1 (informative trials), an auditory-motor working-memory task was designed to investigate the prioritisation of auditory working-memory contents (**Figure 4.6a**). In each trial, two vowel sounds were sequentially played to participants, and participants were asked to report the pitch of one of the two sounds at the end of each trial.

The experimental script was generated using the Psychophysics Toolbox version 3.0.18 (Brainard, 1997) on Matlab 2022a (The Mathworks Inc., Natick, NA, USA). The task was displayed on a monitor (Dell U2312HM; 1920x1080 pixels resolution; 100 Hz refresh rate) while participants sat ~60 cm away from it. For the duration of the study, participants wore Beats EP wired headphones (model A1746) covering both ears. Volume was kept constant across participants (50% of the computer's audio-device volume) and tones of different frequencies were matched in loudness using the ISO226 Equal-Loudness-Level Contour Signal (Tackett, 2024). All sounds were played at a sampling rate of 48 kHz.

At the beginning of each trial, participants heard two vowel sounds (a: /*æ*/ or i: /iː/), each of which lasted 400 ms. The sounds were played sequentially with a 500 ms delay in between and each sound was played over one ear (left or right). During this encoding stage, a white fixation cross was displayed on the screen (14 pixels). The vowel sounds (a or i) varied in their pitch (low or high). Within the low and high pitch conditions, the specific frequency of the sound was drawn from one out of three possible frequencies. These were equally spaced in a logarithmic scale (low-pitch: 70 Hz, 95.4 Hz, 130 Hz; high-pitch: 190 Hz, 217.94 Hz, 250 Hz). The low- and high-pitch conditions were rendered distinguishable by leaving a larger space between the highest low-pitch sound and the lowest high-pitch sound. Sound identity (vowel; a vs i), location (left vs right), order (first vs second), and pitch (high vs low) were counterbalanced such that participants heard sounds with all possible feature combinations. Importantly, sound location and pitch were manipulated orthogonally, such that the high-pitch and low-pitch sounds were equally likely to be played through the left and right ear[7].

Following encoding, there was a delay of 750 ms during which the white fixation cross remained on the screen, and nothing was played through the headphones. Subsequently, a vowel appeared on the centre of the screen for 200 ms (retro-cue).

[7] This simulates the orthogonal manipulation of bar location and tilt in Experiment 1. Here, sound location would correspond to bar location in Experiment 1 and sound pitch (low vs high) would correspond to bar tilt (left vs right) in Experiment 1.

The displayed vowel corresponded to one out of the two played vowels (a or i), had a height of 38 pixels, and was coloured white. Both vowels were displayed as retro-cues in the same number of trials per block.

In half of the trials, the response probe appeared 2 s after cue offset (*short* trials; 50%). In the other half of the trials, the response probe appeared 4 s after cue offset (*long* trials; 50%). During the post-cue delay (short and long), only a white, central fixation cross remained on the screen, and nothing was played through the headphones.

Crucially, two pieces of information predicted which of the two sounds would be probed at the end of the trial with a validity of 80%: 1) the identity of the retro-cue (vowel); and 2) the duration of the delay between the cue and the probe. When the delay following the cue was short (2 s), participants were prompted to report the pitch of the cued sound at the end of the trial (80% validity). Alternatively, in trials with a long delay (4 s), participants were required to report the pitch of the other (uncued) sound (80% validity). In 20% of short and long trials, the retro-cue was misleading (invalid), and participants were probed about the opposite, unpredicted sound. In short invalid trials, the uncued sound (unexpected) was probed; in long invalid trials, the cued sound (unexpected) was probed. Therefore, participants were encouraged to attend to the retro-cue and to track the duration of the subsequent delay to know which of the two sounds they would be asked to report.

Following the delay, a vowel appeared in the centre of the screen (probe) prompting participants to report the pitch of the vowel-matching sound (**Figure 4.6a**). To this end, participants used the "F" and "J" keys on the keyboard with their left and right index fingers respectively. Importantly, the pitch of the probed sound determined the hand of the required response. Low-pitch items required a left-hand response (F key), and high-pitch items required a right-hand response (J key). Upon response initiation, participants heard one of three pure tones with a low (70 Hz, 95.4 Hz, 130 Hz) or a high (190 Hz, 217.9 Hz, 250 Hz) pitch through both ears (tone duration: 500 ms). Key presses caused other tones to be played such that participants could orderly circle around the three tones by pressing the response key again and again. These tones matched the pitch of the vowel sounds. Participants were instructed to press the space bar when the tone they heard matched the pitch of the probed vowel. Importantly, low-pitch pure tones could only be heard by pressing on the F key and high-pitch pure tones by pressing on the J key. Additionally, the response key could not be changed once a response was initiated. Participants were instructed to report the pitch as quickly and accurately as possible. They had a maximum of 5 s to respond from probe onset.

Participants were given feedback on their performance. If they responded with the correct key (F for low-pitch sounds and J for high-pitch sounds) and reported the correct pitch, they saw the message "Correct target!". Alternatively, if they responded with the correct key but did not correctly report the specific pitch, they saw "Correct side but wrong pitch!". If participants responded with the incorrect key, they saw "Wrong target!". If they did not respond, they saw "Too slow!". All feedback appeared centrally in white letters and was displayed for 500 ms. ITIs were sampled randomly from a uniform distribution between 1250 and 1750 ms. During each ITI, a white fixation cross was displayed centrally.

Participants completed 7 blocks of this task of 32 trials each for a total of ~1 h. Between each block, participants had the chance to rest. Before starting the experiment, participants were walked through the instructions of the task. Additionally, they practised the pitch report procedure by circling around the low-pitch and high-pitch sounds with their respective keys. Before starting the experiment, they practiced the task procedure for at least one block.

4.3.2.3 Behavioural data analysis

Behavioural data were analysed as detailed in Experiment 1. RT was defined as the time from probe onset until response initiation. Two different metrics of accuracy were calculated. Side accuracy referred to the proportion of trials in which participants correctly discriminated the pitch (low vs high) of the probed sound. Given that there were two possible pitch conditions (low vs high), chance level for side accuracy was 50%. Tone accuracy was estimated as the proportion of trials in which the specific frequency of the sound was correctly reported, out of all the trials where pitch was successfully discriminated. Given that there were three possible frequencies in each pitch condition, chance level for tone accuracy was 33.4%.

Trials without a response and trials with RTs faster than 100 ms were removed from further analyses. Additionally, trials in which participants did not correctly discriminate between high or low pitch were not included in RT and side accuracy analyses. This resulted in the exclusion of an average of 0.56% trials (SD: 0.92%).

The statistical significance of the dependent variables of interest (RT, side accuracy, and tone accuracy) was tested using repeated-measures ANOVAs with validity (valid vs invalid) and duration (short vs long) as factors. The metric of effect size was η^2 and the within-subject SEM was quantified using the normalised data (Morey, 2008). Bonferroni-corrected paired-samples t-tests were used for unplanned post-hoc comparisons and the effect size was reported as Cohen's d.

4.3.2.4 Eye-tracking data analysis

Participants were asked to keep their eyes on the centre of the screen for the duration of the task. Eye-tracking was recorded as in Experiment 1. Participants performed an eye-tracking calibration task before the first block of the experiment. Additional calibration tasks were performed between blocks if ocular drift was noticed.

The eye-tracking signal was pre-processed as detailed in Experiment 1. In Experiment 2, horizontal and vertical gaze position were analysed further. The data were epoched from 500 ms before to 2500 ms (short) or 4500 ms (long) after cue onset. Trials with eye movements exceeding 125 pixels were removed from further analyses. Additionally, trials with RTs below 100 ms or with incorrect responses (side accuracy) were discarded from further analyses. An average of 31.6% of trials (SD: 14.89%) were excluded, most of which contained large eye movements.

The time course of the horizontal and vertical gaze position in each trial was smoothed with a 60-ms moving window. Subsequently, the epochs were cropped between 200 ms before and 2200 ms (short) or 4200 ms (long) after cue onset to remove any smoothing-related edge artefacts. Finally, the average baseline activity (-200-0 ms), was subtracted from each epoch.

Leftward and rightward gaze-position time courses were compared between trials where a sound from the left or the right was cued (**Figure 4.7a**). Upward and downward gaze-position time courses were compared between trials where a low-pitch vs high-pitch sound was cued (**Figure 4.7b**). Cluster-based permutation testing was used to statistically compare the leftward and rightward horizontal gaze-position time courses and the upward and downward vertical gaze-position time courses, as detailed in Experiment 1.

4.3.3 Results

Experiment 2 investigated whether the prioritisation of contents within auditory working memory was flexible and temporally tuned. Additionally, it tested for the presence of systematic gaze-biases accompanying shifts of auditory internal attention as a function of stimulus location and pitch.

4.3.3.1 Behavioural results

If participants effectively prioritised each of the relevant working-memory contents at the expected times, their responses should be faster in both short and long valid-retro-cue trials compared to invalid-retro-cue trials. A repeated-measures ANOVA of RT with validity and duration as factors confirmed a main effect of validity ($F(1,23) = 6.07$, $^{*}p = .02$, $\eta^2 = .004$), a main effect of duration ($F(1,23) = 10.01$, $^{**}p = .004$, $\eta^2 = .038$), and no interaction between the factors ($F(1,23) = .18$, $p = .68$, $\eta^2 < .000$ **Figure 4.6b**). These results confirmed that participants' responses were systematically faster in trials with valid vs invalid cues. This suggested that the relevant auditory contents were prioritised in a temporally tuned fashion. Additionally, participants were faster in long than short trials.

An ANOVA of side accuracy with validity and duration as factors revealed a main effect of duration ($F(1,23) = 16.66$, ***$p < .001$, $\eta^2 = .034$; **Figure 4.6c**), showing participants to be more accurate in short trials. No main effect of validity was found ($F(1,23) = .008$, $p = .98$, $\eta^2 < .000$), but an interaction between the factors ($F(1,23) = 10.2$, **$p = .004$, $\eta^2 = .018$) occurred. Bonferroni-corrected post-hoc t-tests revealed that participants were similarly accurate in valid and invalid short trials ($t(29) = -2.56$, $p = .08$, $d = .52$) and long trials ($t(29) = 1.9$, $p = .28$, $d = .39$). Participants were more accurate in short invalid trials than long invalid trials ($t(29) = 3.98$, *$p = .04$, $d = .81$) but this effect was absent in valid trials ($t(29) = 1.4$, $p = .72$, $d = .29$). These results suggested that participants were significantly less accurate in long invalid trials than short invalid trials. Nevertheless, no evidence was found for increased accuracy as a function of validity.

Finally, an ANOVA of tone accuracy with the same factors as above revealed a main effect of duration ($F(1,23) = 12.69$, **$p = .002$, $\eta^2 = .02$). No main effect of validity ($F(1,23) = 2.04$, $p = .17$, $\eta^2 = .002$) or interaction between the factors ($F(1,23) = 1.88$, $p = .18$, $\eta^2 = .003$; **Figure 4.6d**) occurred. Together, these findings revealed that participants were significantly more accurate in short trials than long trials, but accuracy performance was not improved by cue validity.

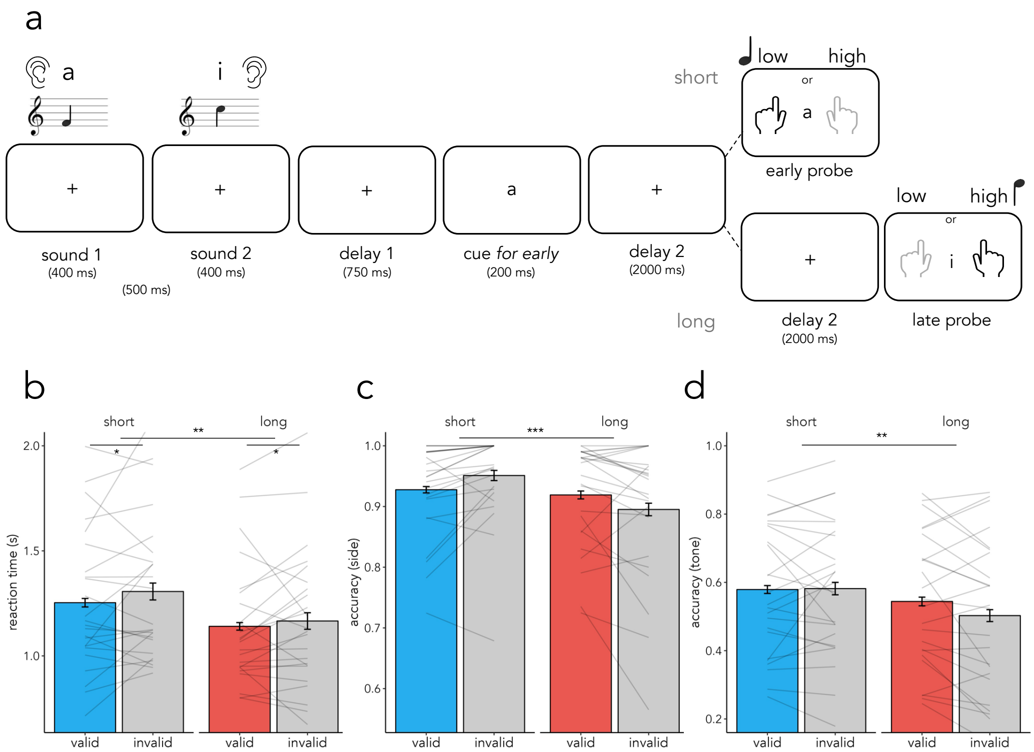


Figure 4.6. Auditory experiment: task design and behavioural results. a) Trial schematic. Two vowel sounds were played sequentially at encoding (one on the left and the other on the right ear; one low-pitch and the other high-pitch with location and pitch being orthogonally manipulated). After a delay, a retro-cue matching the identity of one of the two vowels was shown. If the delay after cue offset was short (2 s), participants were probed to report the cued item in 80% of trials (valid: 80%, invalid: 20%). Alternatively, if the delay was long (4 s), they had to report the other (uncued) item in 80% of trials (valid: 80%, invalid: 20%). b) Reaction time (s), time from probe onset to response initiation, in valid and invalid and short and long trials. c) Side accuracy, proportion of trials in which pitch (low vs high) was correctly discriminated, in valid and invalid and short and long trials. d) Tone accuracy, proportion of trials in which the correct tone was reported, in valid and invalid and short and long trials. *RT (s)*: $M_{val/short}$: 1.25, $SD_{val/short}$: .33, $M_{inval/short}$: 1.3, $SD_{inval/short}$: .35, $M_{val/long}$: 1.14, $SD_{val/long}$: .29, $M_{inval/long}$: 1.17, $SD_{inval/long}$: .33; *Side accuracy:* $M_{val/short}$: .93, $SD_{val/short}$: .08, $M_{inval/short}$: .95, $SD_{inval/short}$: .35, $M_{val/long}$: .92, $SD_{val/long}$: .09, $M_{inval/long}$: .9, $SD_{inval/long}$: .11. *Tone accuracy:* $M_{val/short}$: .58, $SD_{val/short}$: .19, $M_{inval/short}$: .58, $SD_{inval/short}$: .2, $M_{val/long}$: .54, $SD_{val/long}$: .2, $M_{inval/long}$: .5, $SD_{inval/long}$: .22. Thin grey lines represent individual participants, error bars represent the SEM, grey represents invalid trials and colours depict valid trials (red: short, blue: long).

4.3.3.2 Eye-tracking results

The prioritisation of stimulus locations in visual working memory leads to small biases in gaze position in the direction of the internally selected item (e.g., Liu et al., 2022; van Ede et al., 2019b, 2021). In the present study, selecting a sound location was predicted to lead to similar biases in horizontal gaze position. Additionally, shifting from prioritising one sound location to the other was hypothesised to be accompanied by a shift in the direction of this gaze bias (see **Figure 4.5**). Using eye-tracking, the average horizontal gaze position locked to retro-cue onset was estimated as a function of which location was cued (**Figure 4.7a**). This revealed no statistically significant clusters in horizontal gaze position as a function of cued location.

The pitch of sounds has been hypothesised to be spatially represented along the vertical axis with higher-pitch sounds corresponding to higher positions and lower-pitch sounds to lower locations in space (C. C. Pratt, 1930). Therefore, cueing a high-pitch sound may lead to an upward gaze bias while cueing a low-pitch sound might result in a downward gaze bias. To test this possibility, the average vertical gaze position was locked to retro-cue onset as a function of the pitch of the cued sound (high vs low; **Figure 4.7b**). This comparison revealed no statistically significant clusters in vertical gaze position as a function of cued pitch.

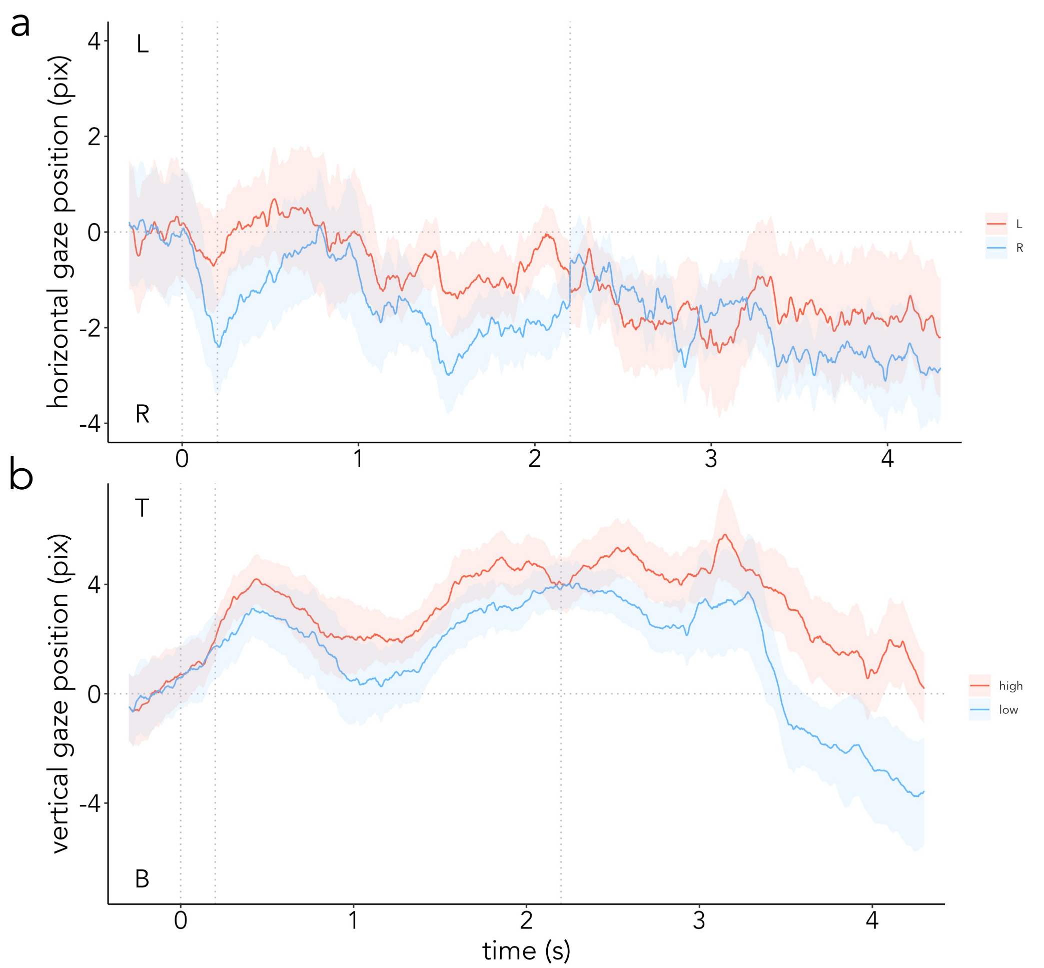


Figure 4.7. Auditory experiment: horizontal and vertical gaze position as a function of cued vowel location and pitch locked to retro-cue onset. a) Participant-average horizontal gaze position (in pixels) when a sound on the left (blue) vs on the right (red) was cued, locked to retro-cue onset. b) Participant-average vertical gaze position (in pixels) when a low-pitch sound (blue) vs a high-pitch sound (red) was cued, locked to retro-cue onset. Shaded areas represent the SEM, and vertical dotted lines represent (from left to right), retro-cue onset and offset and time of probe appearance in early trials. The first part of the time courses (0-2.2 s) contains both short and long trials, and the second part (2.2-4.2) contains long trials only. L, R, T, and B refer to the left, right, top and bottom part of the screen respectively.

4.3.4 Discussion

The present study shows that the prioritisation of auditory contents in working memory flexibly speeds response times in a temporally tuned fashion. Interestingly, the internal attention shifts in this task were not accompanied by shifts in gaze position related to the location or pitch of the attended sounds in working memory.

In this study, response times revealed that participants were faster when responding to targets at the expected times. Participants were systematically faster at responding to validly cued sounds in short trials, suggesting that they used retro-cues to prioritise the relevant sounds and/or prospective-responses in working memory (Backer et al., 2015, 2020; Backer & Alain, 2012; Fan et al., 2021; Lim et al., 2015). Crucially, the present study showed reaction-time benefits from internally driven auditory temporal expectations. This design feature arguably better simulates everyday situations compared to studies using external cues.

The present study revealed no systematic differences in accuracy between validly and invalidly cued sounds, suggesting that prioritising working-memory contents did not enhance pitch discriminability. Admittedly, participants' discrimination accuracy in this study was highly variable. Some participants discriminated between high- and low-pitch sounds with near-perfect accuracies, while others had substantial difficulty with discrimination (**Figure 4.6c**). Reproducing the specific pitch of high- and low-pitch sounds by choosing the corresponding pure tone also yielded a large variance in accuracies, with some participants' performance nearing chance level (**Figure 4.6d**). This accords with the relatively poor ability of human participants to identify or reproduce pitch (Levitin & Rogers, 2005). The large variability in performance may have occluded some of the underlying behavioural patterns in this study.

The inconsistencies between RT and accuracy results may reflect the fact that retro-cues and temporal expectations in this task modulated response preparation but not perceptual discriminability of sounds. This is consistent with the results in Experiment 1 and with other studies suggesting that internal attention renders working-memory representations "action-ready" (Boettcher et al., 2021; Formica et al., 2021; González-García et al., 2020; Henderson et al., 2022; Heuer et al., 2020; Kikumoto et al., 2022; Myers et al., 2017; Rösner et al., 2022; Trentin et al., 2023; van Ede et al., 2019a). However, internal attention is also known to selectively enhance the quality or accessibility of working-memory contents (for review see van Ede & Nobre, 2023), and several studies have found that prioritising auditory working-memory contents influences perceptual processing (e.g. Backer & Alain, 2012).

In this task, participants' responses were systematically faster in long trials than in short trials. This probably reflects increased preparedness to respond following a longer delay (e.g., Los, 2010). However, participants' responses were also consistently more inaccurate in long trials, which could reflect a time-related decay in working-memory contents (Baddeley, 1986) or a speed-accuracy trade-off.

Performance in Experiment 2 differed substantially from that in Experiment 1. On average, participants were slower, more inaccurate and more variable at reporting auditory pitch than visual orientation. Additionally, six participants had to be excluded from further analyses altogether due to chance performance in the auditory task. This suggests that the translation from the visual (Experiment 1) to the auditory modality (Experiment 2) was not wholly successful. Specifically, I tried to transpose some of the key features of the visual-motor working-memory task to an auditory design. First, the orthogonal manipulation of location and action was aimed at independently tracking the prioritisation of sensory features (location) and motor-related content (action) in auditory working memory. Moreover, the incorporation of a pitch reproduction response corresponded to the continuous orientation reports in Experiment 1. Finally, the reported feature (pitch) was kept independent from the cued content (vowel) and location. However, the one-to-one translation from a visual to an auditory design may have resulted in an overly complex auditory task, which participants struggled to perform successfully. In turn, this probably resulted in a lack of sensitivity to detect consistent behavioural patterns in this study. In future experiments, the one-to-one mapping approach should be replaced with a more nuanced translation.

In contrast to the visual-motor task in Experiment 1 and other studies (Liu et al., 2022; van Ede et al., 2019b; van Ede et al., 2021), the present study suggests that sound location prioritisation did not result in spatially specific gaze biases. While visual stimuli are distributed spatially in visual scenes, auditory information is contained in time-varying signals (e.g., amplitude and frequency modulation). Sound location is computed during a subsequent processing step, from the differences in the time at which auditory signals reach each of the ears (for review see Noyce et al., 2023). Consistently, auditory contents in working memory may not follow a spatial configuration. Given this non-spatial arrangement, the prioritisation of auditory contents may not engage the oculomotor system, which could explain the present results. However, the null result in the present study may also be the product of task difficulty and variable performance strategies. Consequently, further research efforts should be devoted to investigating whether auditory internal attention engages the oculomotor system.

Moreover, the present study provides no evidence that the internal selection of auditory contents in working memory, as measured with vertical gaze biases, is modulated by pitch. It has been repeatedly shown that humans and other species tend to associate high-pitch sounds with higher positions in space and low-pitch sounds with lower positions (e.g., Pratt, 1930). Based on this, the present study tested whether internal prioritisation of a high-pitch sound would lead to an upwards gaze-bias and vice versa. Contrary to my predictions, no biases in vertical gaze position were found as a function of the pitch of the cued item. While this null finding might reflect a genuine result, it could also be the product of participants' poor discrimination of high and low pitch in this task. Consequently, further research using more sensitive designs could test this question further.

Auditory working memory serves key cognitive functions that require fine temporal control, such as speech. Given the requirement of a flexible and temporally tuned prioritisation of auditory working-memory contents, I speculate that some of the null findings observed in the present study may have been related to the insufficient sensitivity of the present task. However, it is also probable that the neural systems responsible for orienting attention within auditory working memory are not the same as those involved in visual working memory. This would be in line with the differences reported between external auditory and visual attention (Braga et al., 2013; Michalka et al., 2015, 2016; Noyce et al., 2017). Therefore, the eyes may not be the peripheral effectors most strongly affected by internal auditory attention. Instead, it may harness the functional circuitry of other systems such as the speech production system.

An interesting open question is whether the prioritisation of hand actions in auditory working memory is linked to a temporally specific contralateral attenuation of mu-beta activity (see Experiment 1; Schneider et al., 2017; van Ede et al., 2019a). The time course of action selection, together with its topography would provide interesting insights into how selecting the same action may be different depending on the visual vs auditory nature of the task. Alpha attenuation has been observed during the allocation of external attention to specific auditory locations and features (Bonacci et al., 2019, 2020; Todorovic & de Lange, 2012; Wöstmann et al., 2021). Therefore, a related question for further investigation is whether selecting auditory contents in working memory is linked to a reduction in alpha-frequency activity in the present design.

In summary, the aim of Experiment 2 was to investigate whether and how auditory contents in working memory were flexibly prioritised as a function of time-varying expectations. To do so, I translated some of the key features of the task in Experiment 1 into the auditory modality. While auditory contents in working memory seemed to be flexibly and dynamically prioritised, much remains to be learned about the mechanisms underlying this process.

5 General discussion

Throughout this thesis, different facets of how temporal structures in the environment modulate perception and attention have been presented, explored, and discussed. Specifically, the present thesis investigated how expectations that emerge from environmental regularities drive perception and attention in combination with other guidance signals such as goal relevance. This work contributes to a growing body of knowledge elucidating the nuanced ways in which perception and attention (internal and external; visual and auditory) are tuned to environmental regularities.

Replicating and extending prior findings, **Chapter 2** of this thesis reported that feature regularities in the context of an ongoing task systematically biased perception of other visual features. Moreover, feature regularities unfolding over different timescales were found to modulate perception jointly. This chapter additionally reported that while general task performance was influenced by guidance signals such as predictability and relevance of the regular feature, perceptual biases were not consistently affected.

Chapter 3 transitioned from feature regularities to temporal regularities. I designed a task to capture two ways in which temporal regularities guide attention in natural behaviour: the incidental learning of temporal regularities that form temporal expectations; and the flexible prioritisation of predictable times based on task goals. The studies in **Chapter 3** found that selective temporal attention can be deployed flexibly to predictable time points to enhance performance in the absence of spatial and motor certainty. The effects generalised across experiments in the visual and auditory modalities.

Chapter 4 extended the inquiry to internal temporal attention. I tested whether both sensory and motor contents in visual working memory were modulated flexibly and dynamically based on temporal expectations. Using neural measures, I revealed that motor contents in working memory were flexibly prioritised as internal attention shifted between objects and their corresponding response hand according to temporal expectations. The overall flexible pattern of motor modulation was similar to sensory modulation according to object location. However, analyses of the time courses showed that motor and sensory modulatory functions were not strictly temporally bound, suggesting that multiple modulatory processes run in tandem. Moreover, using an auditory task, I found that auditory contents in working memory could also be flexibly prioritised according to dynamically evolving expectations.

5.1 Guidance signals

Across all the empirical studies in this thesis, the joint effects of two guidance signals (expectation and relevance) on perception and attention were investigated. By manipulating the relevance of feature and temporal expectations, **Chapters 2** and **3** found that perception and external attention, respectively, were influenced by changes in the relevance of expectations. **Chapter 2** revealed that while task performance was influenced by the predictability and relevance of the regular feature, these did not consistently affect perceptual biases. In **Chapter 3**, the relevance of features with different temporal probability structures was manipulated trial by trial. Across three experiments that differed in several features including sensory modality (visual and auditory), different temporal expectations were flexibly used to guide external attention. Finally, in **Chapter 4**, the relevance of different sensory (visual and auditory) and action-related working-memory contents changed as a function of dynamically evolving temporal expectations. This study confirmed that contents were prioritised flexibly and in a temporally tuned fashion on the basis of changing probabilities of different contents being probed.

While debates about the effects of guidance signals on sensory processes exist (Firestone & Scholl, 2014, 2016; Pylyshyn, 1999), the consensus is that ongoing perception and attention are profoundly influenced by memories across different timescales (Chun, 2000; Chun et al., 2011; Fiser & Lengyel, 2022; Hutchinson & Turk-Browne, 2012; Nobre & Stokes, 2019; Schapiro & Turk-Browne, 2015), expectations (Clark, 2013; de Lange et al., 2018; Gilbert & Li, 2013; Nobre & van Ede, 2018; Summerfield & de Lange, 2014), relevance (Nobre, 2018; Nobre & Kastner, 2014; Summerfield & de Lange, 2014), motivations (Nobre, 2018; Pessoa, 2009, 2015; Serences, 2008), and possibly other control signals.

In the case of external attention, unique combinations of sensory inputs and guidance signals are thought to be integrated in frontoparietal networks and their connections with other cortical and subcortical areas. In turn, frontoparietal networks feed back into in sensory, motor, and higher-level areas to modulate their activity (Mesulam, 1981, 1990, 1999; Nobre, 2018; Nobre & Mesulam, 2014). Consistently, in temporal attention, identical tasks with different purposes (perceptual vs motor) have been shown to engage common nodes of the frontoparietal network (e.g., left IPS; Davranche et al., 2011), which are differentially connected with sensory and motor areas, respectively, depending on task purpose. Moreover, perceptual and motor purposes of temporal expectations result in different downstream modulations, targeting sensory and motor activity, respectively (Shalev et al., 2019; van Ede et al., 2020). Here, **Chapter 4** suggests that internal attention can have dissociable modulatory effects on sensory and motor systems, respectively, depending on when and for how long they are relevant.

From a broader perspective, the tasks in the present thesis encouraged participants to respond "rapidly and accurately", thus emphasizing the implicit goal of "optimising" task performance. Nevertheless, several everyday tasks encourage learning, exploration, and other goals instead of optimising performance. Therefore, an additional dimension which is beyond the scope of the present thesis is to investigate how the effects of perception and attention may change according to the overarching purpose of the tasks (Nobre, 2018).

5.2 TIME AS THE QUESTION

Many studies have found that temporal (external) attention modulates spatial and motor processes. Invasive recordings in non-human primates have revealed temporally specific changes in the firing rates of spatially selective neurons (Ghose & Bearl, 2010; Ghose & Maunsell, 2002) and motor neurons (Heinen & Liu, 1997; Janssen & Shadlen, 2005; Kilavik & Riehle, 2010; Lucchetti & Bon, 2001; Riehle et al., 1997). Similar modulations can be approximated from non-invasive neurophysiology and stimulation studies in humans (e.g., Rohenkohl & Nobre, 2011; van Elswijk et al., 2007). Moreover, these changes seem to result in behavioural benefits such that temporal expectations act by increasing motor preparation (Heideman et al., 2018b, 2018a, 2018c; O'Reilly et al., 2008; Thomaschke & Dreisbach, 2013) and/or by interacting with spatial attention (Doherty et al., 2005; Nobre & Rohenkohl, 2014; Seibold et al., 2020).

Some studies have found modulations of other sensory features by temporal attention (Anderson & Sheinberg, 2008; Jaramillo & Zador, 2011; Lima et al., 2011; Warren et al., 2014). However, they have typically not manipulated spatial and motor uncertainty. Therefore, potential modulations of temporal attention on non-spatial and non-motor processes could not be entirely isolated. In this light, **Chapter 3** of the present thesis aimed at gauging the effects of temporal attention on visual and auditory features while these were isolated from spatial and action-related attributes. Behaviourally, the flexible allocation of attention on the basis of feature-temporal expectations facilitated performance in the absence of spatial and motor certainty. Future studies using non-invasive neurophysiology should track the time courses of modulation of task-relevant and -irrelevant features that are temporally predictable and unpredictable. This will provide further insights into the time courses of attentional modulation of sensory features based on different guidance signals in the face of spatial and motor uncertainty.

In contrast, **Chapter 4** builds on what is known about the modulatory effects of external attention on spatial and motor attributes to investigate whether internal attention harnesses similar principles. With this aim, locations and actions associated with items in working memory were manipulated orthogonally. Their prioritisation time courses were monitored with high temporal resolution using EEG and eye-tracking. This study reported that the prioritisation of task-relevant locations and actions in working memory resulted in location-specific and effector-specific reductions in alpha- and mu-beta-frequency activity, respectively. These modulations were tuned to the times at which each location and action was expected to become relevant. Together, these findings show that, similar to what has been reported in external attention, internal attention can modulate spatial and motor activity at specific times. This is in line with several other studies which have identified similarities in the underlying mechanisms of internal and external attention (Griffin & Nobre, 2003; Nobre et al., 2004; Panichello & Buschman, 2021).

In **Chapters 3** and **4**, temporal regularities were bound to other stimulus attributes. **Chapter 3** demonstrated that these need not be spatial or motor. Instead, attention could be oriented to temporally expected colours or sound frequencies thus facilitating their detection. In **Chapter 4**, the sensory attributes of the prioritised stimulus (location and colour) and the associated actions were temporally structured. In turn, internal attention modulated activity related to spatial and motor codes in a temporally tuned fashion. One outstanding question, then, is whether temporal structures need to latch onto other stimulus attributes to be picked up by the brain (Nobre & van Ede, 2018).

Even assuming they did, how this may occur is an unsolved puzzle. For example, is there a clocking mechanism that activates attention's modulatory effects at the relevant times? How would this timekeeping mechanism be implemented in the brain? Would this be orchestrated by frontoparietal networks, by subcortical areas with widespread and direct cortical projections, or through a completely different mechanism? The distinction between implicit and explicit timing[8] may be key in arbitrating between these options (Coull & Nobre, 2008). Does the use of temporal information to guide other cognitive processes build on neural circuits dedicated to timekeeping, provided that these exist?

Generally, the mechanistic conceptions of timing can be categorised into proposals which suggest that there are dedicated timing circuits in the brain (Gibbon et al., 1984; Lashley, 1951; Miall, 1989; Treisman, 1963) and those that propose that timing is an intrinsic property of all brain circuits (Mauk & Buonomano, 2004; Staddon, 2005; Wittmann, 2013; for reviews see Coull et al., 2011; Ivry & Schlerf, 2008; Muller & Nobre, 2014). Within the former group, several candidate areas and processes for timekeeping have been proposed, including the cerebellum (Ivry & Keele, 1989; Ivry & Spencer, 2004) and the basal ganglia (Buhusi & Meck, 2005; Meck, 1996), perhaps through striatal-medial-frontal loops (Coull, 2004; Macar et al., 2006). Within the latter group, Karmarkar and Buonomano (2007) suggested that a temporal metric was calculated locally in each brain area. Alternatively, the entrainment of large-scale neural networks to oscillatory activity could reflect a general mechanism for timing, at least in the case of rhythmic stimuli (Fries, 2005; Lakatos et al., 2008; Schroeder & Lakatos, 2009).

Adding to an already-complicated debate, guidance signals like the ones described above and different sources of temporal regularities seem to engage different neural systems and cognitive processes (Coull & Nobre, 2008; see also Bouwer et al., 2020; Breska & Deouell, 2014; Breska & Ivry, 2018; de la Rosa et al., 2012; Rohenkohl et al., 2011; Shalev et al., 2019; Tal-Perry & Yuval-Greenberg, 2022; Triviño et al., 2011). Therefore, a comprehensive understanding of timing will also need to consider this dimension. As detailed above, the present thesis makes some contributions to this effort.

[8] Implicit timing refers to the use of timing for other cognitive processes, while in explicit timing time is the reported feature.

Research in this thesis provides two key insights into how timing may be used for attention. First, the finding that temporal attention can act flexibly under spatial and motor uncertainty suggests that implicit timing for attention does not exclusively act by modulating spatial and motor processes. Secondly, **Chapter 4** shows that the same temporal expectations lead to dissociable effects on sensory and motor systems, respectively. This provides preliminary evidence that temporal attention may exert different modulatory effects with distinct timings and durations, depending on the temporal structure of the task. Thus, a multitude of timing signals may be needed to pace the prioritisation of different contents (sensory and action-related) in distinct neural systems.

5.3 TIME AS THE ANSWER

In addition to being the thematic undercurrent of this thesis, the temporal dimension has also been considered in its methodology. Despite their shortcomings, the designs presented in this thesis have attempted to assimilate some of the complexities of time. The task in **Chapter 2** is a continuous stream of orientation reports in which regularities unfold over different timescales: session, block, and inter-trials contingencies. **Chapter 3** brings the investigation of temporal attention to an extended design where several task-relevant and -irrelevant targets, together with distractors and masks, unfold dynamically over time. This adds to a growing body of literature which has incorporated the temporal dimension into tasks investigating attention, such as visual search (e.g., Boettcher et al., 2022; Salet et al., 2021; Shalev et al., 2022). Extended tasks highlight the methodological challenges of the temporal dimension in which several time-varying signals and effects co-exist and interact. For example, in **Chapter 3**, incidentally learned feature-temporal associations co-exist with the hazard function (Luce, 1991) and sequential effects between past responses and current target timings (Los, 2010). Nevertheless, embracing the complexity of the temporal dimension is also intriguing and essential to gain a comprehensive understanding of cognitive processes like attention.

Conversely, a limitation of the present thesis is the usage of temporally discrete proxies of task performance like RT, accuracy, or report error. An important step forward will come from the adoption of temporally resolved readouts of behaviour (e.g., EMG, mouse-tracking, and eye-tracking) together with modelling approaches that capture temporally extended processes (e.g., drift-diffusion modelling). Consistently, in **Chapter 4**, temporally resolved proxies of behaviour (eye-tracking) and brain activity (EEG frequency-specific activity) were harnessed. Nevertheless, these signals were averaged across trials, an approach that can miss out on key temporal features of the data. For example, the short-lived nature of beta-frequency (13-30 Hz) activity and the relevance of its temporal profile has long been ignored due to trial-averaging (Feingold et al., 2015; Jones, 2016; Lundqvist et al., 2016, 2024; Quinn et al., 2019; Shin et al., 2017; van Ede et al., 2018). Nevertheless, methods which underscore the temporal motifs in neurophysiological data, such as Empirical Mode Decomposition (EMD) and Hidden Markov Models (HMM), have begun to provide important insights about the underlying neural dynamics (Echeverria-Altuna et al., 2022; Heideman et al., 2020; Quinn et al., 2019). Thus, analysis approaches that embrace the temporal complexity of physiological signals should be utilised (e.g., Bialas et al., 2023; Ruesseler et al., 2023; Vidaurre et al., 2018).

5.4 Lost in translation across sensory modalities

In this thesis, attention is defined as the set of processes responsible for anticipating, prioritising, selecting, routing, integrating, and preparing relevant contents to guide adaptive behaviour (Nobre, 2018). While attention has been studied mostly in the visual modality, auditory contents can also be prioritised by attention[9]. Importantly, attention can be oriented not only to external auditory events (Cherry, 1953; Hillyard et al., 1973; **Chapter 3**) but also to auditory contents in working memory (Backer &

[9] The same holds for contents from other sensory systems and for multimodal contents, which are beyond the scope of the present thesis.

Alain, 2012; **Chapter 4**). Consistently, the present thesis has attempted to test the generalisability of some of its findings about external and internal attention across two sensory modalities: vision and audition.

A conclusion that I draw from this thesis is that the translation of task designs across sensory modalities is a complex and multi-faceted challenge. While stimulus features can be translated across modalities using a one-to-one mapping approach (e.g., colour is replaced by pitch; see **Chapter 3**), this strategy can result in missteps at different stages. For example, while colour discriminability is commonly achieved by selecting colours that are equidistantly spaced in a pseudo-circular perceptual colour space (e.g. CIELab), tone frequencies ought to be logarithmically spaced and corrected for differences in loudness (Tackett, 2024). These disparities influence parameters such as the perceptual distance between targets and distractors which, in turn, affect perception and attention (Geng, 2014).

Moreover, there are fundamental differences in how accurately participants can reproduce colour/orientation and pitch (Levitin & Rogers, 2005), which result in discrepancies in task difficulty as a function of sensory modality. In turn, task difficulty could interact with the guidance signals presented above and result in the engagement of different behavioural strategies and distinct attentional processes at different times. Therefore, one-to-one mappings between modalities do not guarantee the engagement of comparable attentional (and, more broadly, cognitive) processes. In **Chapters 3** and **4**, auditory temporal attention (external and internal) was investigated and contrasted with its visual counterpart. In contrast to what may have been naively expected given the centrality of the temporal dimension to audition, participants' responses were consistently more variable and less accurate in auditory tasks than in visual tasks. In addition to differences in low-level processes such as discriminability, different guidance signals and attentional processes may have been engaged leading to the performance differences.

Additionally, given the precedence of visual designs in this thesis, the auditory tasks may have been visually biased. While visual information is distributed across space, auditory information unfolds over time. Perhaps unsurprisingly, trial-by-trial attention cueing tasks (Posner, 1980) and multiple-stream tasks (Cherry, 1953; Hillyard et al., 1973) emphasize key features of the visual and auditory modality, respectively. While the former manipulates goal-driven flexibility, the latter highlights the continuous temporal unfolding of attention. Arguably, the manipulation of temporal attention using Posner-like tasks orients attention to points in time in a spatially inspired fashion. Attended time-points represent snapshots and not dynamically changing signals. Therefore, more veridical comparisons between auditory and visual attention could be achieved by using ecologically valid signals from each modality. A clear example of a temporally unfolding signal in the visual domain is motion, which could be contrasted with time-varying sounds.

Relatedly, identifying the purposes that (visual and auditory) attention may have evolved to subserve could help steer the development of fine-tuned experimental designs (Cisek, 2007). Arguably, one key feature of auditory attention in humans is to keep track of speech, the main vehicle for human communication. While a lot has been uncovered about how speech is attended (e.g., Ding & Simon, 2012; O'Sullivan et al., 2015; Rieke et al., 1997), its similarities and differences with visual attention, together with the joint prioritisation of multimodal signals remain mysterious (Ahmed et al., 2023).

5.5 Learning over time

The passage of time is responsible for learning and, therefore, for our memories and experiences. Across all the tasks in this thesis, regularities in stimulus features and timings were learned[10] by participants. The specific mechanisms whereby learning may have occurred in the different tasks of the present thesis is unknown, but a few candidate options are discussed below. In **Chapter 2**, participants learned the repeated feature through exposure but, in Experiment 1 and predictable blocks of Experiment

[10] Improvement in performance due to training or exposure (e.g., Fahle & Poggio, 2002).

2, participants were also explicitly instructed about the relevant stimulus contingency. In **Chapter 3**, participants learned the associations between specific features (colour or pitch) and their corresponding timings incidentally through experience.

Speculatively, regularities and associations in these tasks may have been picked up through statistical learning (for reviews see Hutchinson & Turk-Browne, 2012; Schapiro & Turk-Browne, 2015). The implicit learning of associations between adjacent events (associative learning) has been shown to modulate activity in IT and MTL neurons in non-human primates (Miyashita, 1988; Osada et al., 2008; Wirth et al., 2003). Consistently, the learning of regularities in humans has been reported to engage areas such as the MTL, the striatum (Turk-Browne et al., 2009), and the inferior frontal gyrus (IFG; Turk-Browne et al., 2009). Moreover, learning predictive relations between adjacent events seems to specifically engage the hippocampus (Schapiro et al., 2012, 2013, 2014; Turk-Browne et al., 2010). Speculatively, these neural mechanisms may underlie learning in the presented tasks.

Importantly, in **Chapter 3**, feature-temporal associations were learned. In **Chapter 4**, no associative relations between features were present, but participants may have learned to associate the requirement to respond with specific delays. The learning of temporal associations has been comparatively less studied than associations between other features. For example, Cravo and colleagues (2017) found that associations between scenes and target timings facilitated subsequent attentional guidance and modulated known markers of temporal attention such as the CNV. Interestingly, the CNV has been suggested to reflect the engagement of medial frontal areas like the SMA (Nagai et al., 2004) and, more broadly, striatal-medial-frontal loops which are involved in other aspects of timing (e.g., Coull, 2004; Macar et al., 2006). Additionally, learning of temporal intervals has been suggested to involve the cerebellum and/or cortico-thalamic-striatal loops (for review see Breska & Ivry, 2016; Merchant et al., 2013).

5.6 FINAL CONCLUSIONS

Across three empirical chapters and eight experiments, the present thesis has made important contributions to how perception, external attention, and internal attention are tuned to feature and temporal regularities in the environment. Furthermore, this thesis has contributed to the understanding of how different guidance signals concurrently drive perception and attention. Moreover, an effort has been made to generalise these findings across different sensory modalities.

The main conclusions to be drawn from this thesis are the following: 1) perception is modulated by feature regularities across multiple timescales; 2) attention can be oriented flexibly based on feature-temporal expectations in the absence of spatial and motor certainty; 3) the prioritisation of sensory and action-related contents that co-exist in working memory is flexible, temporally tuned, but not necessarily coupled; and 4) guidance signals such as expectation and relevance work in concert to guide attention. In the quest to reach these conclusions, this thesis has been confronted with some of the epistemological and methodological challenges posed by the temporal dimension. On occasion, it has also gotten lost in translation between the visual and the auditory modalities. As a whole, it has furthered our understanding of the ins and outs of how temporal structures in the environment fine-tune cognitive processes such as perception and attention.

6 REFERENCES

Abeles, D., Amit, R., Tal-Perry, N., Carrasco, M., & Yuval-Greenberg, S. (2020). Oculomotor inhibition precedes temporally expected auditory targets. *Nature Communications*, *11*(1), 3524. https://doi.org/10.1038/s41467-020-17158-9

Adrian, E. D., & Matthews, B. H. C. (1934). The Berger rhythm: Potential changes from the occipital lobes in man. *Brain: A Journal of Neurology*, *57*, 355–385. https://doi.org/10.1093/brain/57.4.355

Ahmed, F., Nidiffer, A. R., O'Sullivan, A. E., Zuk, N. J., & Lalor, E. C. (2023). The integration of continuous audio and visual speech in a cocktail-party environment depends on attention. *NeuroImage*, *274*, 120143. https://doi.org/10.1016/j.neuroimage.2023.120143

Aitken, F., Menelaou, G., Warrington, O., Koolschijn, R. S., Corbin, N., Callaghan, M. F., & Kok, P. (2020). Prior expectations evoke stimulus-specific activity in the deep layers of the primary visual cortex. *PLOS Biology*, *18*(12), e3001023. https://doi.org/10.1371/journal.pbio.3001023

Akrami, A., Kopec, C. D., Diamond, M. E., & Brody, C. D. (2018). Posterior parietal cortex represents sensory history and mediates its effects on behaviour. *Nature*, *554*(7692), 368–372. https://doi.org/10.1038/nature25510

Alexi, J., Cleary, D., Dommisse, K., Palermo, R., Kloth, N., Burr, D., & Bell, J. (2018). Past visual experiences weigh in on body size estimation. *Scientific Reports*, *8*(1), 215. https://doi.org/10.1038/s41598-017-18418-3

Amit, R., Abeles, D., Carrasco, M., & Yuval-Greenberg, S. (2019). Oculomotor inhibition reflects temporal expectations. *NeuroImage*, *184*, 279–292. https://doi.org/10.1016/j.neuroimage.2018.09.026

Anderson, B., & Sheinberg, D. L. (2008). Effects of temporal context and temporal expectancy on neural activity in inferior temporal cortex. *Neuropsychologia*, *46*(4), 947–957. https://doi.org/10.1016/j.neuropsychologia.2007.11.025

Androulidakis, A. G., Kühn, A. A., Chen, C. C., Blomstedt, P., Kempf, F., Kupsch, A., Schneider, G.-H., Doyle, L., Dowsey-Limousin, P., Hariz, M. I., & Brown, P. (2007). Dopaminergic therapy promotes lateralized motor activity in the subthalamic area in Parkinson's disease. *Brain : A Journal of Neurology*, *130*(Pt 2), 457–468. https://doi.org/10.1093/brain/awl358

Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception, & Psychophysics*, *74*(1), 146–162. https://doi.org/10.3758/s13414-011-0218-3

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In *The psychology of learning and motivation: II.* (pp. xi, 249–xi, 249). Academic Press. https://doi.org/10.1016/S0079-7421(08)60422-3

Backer, K. C., & Alain, C. (2012). Orienting attention to sound object representations attenuates change deafness. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(6), 1554–1566. https://doi.org/10.1037/a0027858

Backer, K. C., Binns, M. A., & Alain, C. (2015). Neural dynamics underlying attentional orienting to auditory representations in short-term memory. *The Journal of*

Neuroscience : The Official Journal of the Society for Neuroscience, *35*(3), 1307–1318. https://doi.org/10.1523/JNEUROSCI.1487-14.2015

Backer, K. C., Buchsbaum, B. R., & Alain, C. (2020). Orienting Attention to Short-Term Memory Representations via Sensory Modality and Semantic Category Retro-Cues. *Eneuro*, *7*(6), ENEURO.0018-20.2020. https://doi.org/10.1523/ENEURO.0018-20.2020

Baddeley, A. (1986). *Working memory.* (pp. xi, 289). Clarendon Press/Oxford University Press.

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). Academic Press. https://doi.org/10.1016/S0079-7421(08)60452-1

Bae, G.-Y. (2024). Cardinal bias interacts with the stimulus history bias in orientation working memory. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-024-02867-w

Balke, J., Rolke, B., & Seibold, V. C. (2021). Reduction of temporal uncertainty facilitates stimulus-driven processes in spatial selection. *Biological Psychology*, *159*, 108028. https://doi.org/10.1016/j.biopsycho.2021.108028

Bang, J. W., & Rahnev, D. (2017). Stimulus expectation alters decision criterion but not sensory signal in perceptual decision making. *Scientific Reports*, *7*(1), 17072. https://doi.org/10.1038/s41598-017-16885-2

Barbosa, J., & Compte, A. (2020). Build-up of serial dependence in color working memory. *Scientific Reports*, *10*(1), 10959. https://doi.org/10.1038/s41598-020-67861-2

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bauer, A.-K. R., van Ede, F., Quinn, A. J., & Nobre, A. C. (2021). Rhythmic Modulation of Visual Perception by Continuous Rhythmic Auditory Stimulation. *The Journal of Neuroscience*, *41*(33), 7065. https://doi.org/10.1523/JNEUROSCI.2980-20.2021

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, *9*(10), 7–7. https://doi.org/10.1167/9.10.7

Beck, M. R., Hong, S. L., van Lamsweerde, A. E., & Ericson, J. M. (2014). The Effects of Incidentally Learned Temporal and Spatial Predictability on Response Times and Visual Fixations during Target Detection and Discrimination. *PLoS ONE*, *9*(4), e94539. https://doi.org/10.1371/journal.pone.0094539

Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv Für Psychiatrie Und Nervenkrankheiten*, *87*(1), 527–570. https://doi.org/10.1007/BF01797193

Bialas, O., Dou, J., & Lalor, E. C. (2023). mTRFpy: A Python package for temporal response function analysis. *Journal of Open Source Software*, *8*(89), 5657. https://doi.org/10.21105/joss.05657

Bledowski, C., Rahm, B., & Rowe, J. B. (2009). What 'works' in working memory? Separate systems for selection and updating of critical information. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(43), 13735–13741. https://doi.org/10.1523/JNEUROSCI.2547-09.2009

Bliss, D. P., Sun, J. J., & D'Esposito, M. (2017). Serial dependence is absent at the time of perception but increases in visual working memory. *Scientific Reports*, *7*(1), 14739. https://doi.org/10.1038/s41598-017-15199-7

Blondé, P., Kristjánsson, Á., & Pascucci, D. (2023). Tuning perception and decisions to temporal context. *iScience*, *26*(10), 108008. https://doi.org/10.1016/j.isci.2023.108008

Boboeva, V., Pezzotta, A., Clopath, C., & Akrami, A. (2023). *From recency to central tendency biases in working memory: A unifying network model* [Preprint]. elife. https://doi.org/10.7554/eLife.86725.1

Boettcher, S. E. P., Gresch, D., Nobre, A. C., & van Ede, F. (2021). Output planning at the input stage in visual working memory. *Science Advances*, *7*(13), eabe8212. https://doi.org/10.1126/sciadv.abe8212
Boettcher, S. E. P., Shalev, N., Wolfe, J. M., & Nobre, A. C. (2022). Right place, right time: Spatiotemporal predictions guide attention in dynamic visual search. *Journal of Experimental Psychology: General*, *151*(2), 348–362. https://doi.org/10.1037/xge0000901
Bonacci, L. M., Bressler, S., & Shinn-Cunningham, B. G. (2020). Nonspatial Features Reduce the Reliance on Sustained Spatial Auditory Attention. *Ear and Hearing*, *41*(6), 1635–1647. https://doi.org/10.1097/AUD.0000000000000879
Bonacci, L. M., Dai, L., & Shinn-Cunningham, B. G. (2019). Weak neural signatures of spatial selective auditory attention in hearing-impaired listeners. *The Journal of the Acoustical Society of America*, *146*(4), 2577. https://doi.org/10.1121/1.5129055
Boshra, R., & Kastner, S. (2022). Attention control in the primate brain. *Current Opinion in Neurobiology*, *76*, 102605. https://doi.org/10.1016/j.conb.2022.102605
Bouwer, F. L., Honing, H., & Slagter, H. A. (2020). Beat-based and Memory-based Temporal Expectations in Rhythm: Similar Perceptual Effects, Different Underlying Mechanisms. *Journal of Cognitive Neuroscience*, *32*(7), 1221–1241. https://doi.org/10.1162/jocn_a_01529
Brady. (1998). A Theoretical and Empirical Review of the Contextual Interference Effect and the Learning of Motor Skills. *Quest*, *50*(3), 266–293. https://doi.org/10.1080/00336297.1998.10484285
Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision*, *11*(5), 4–4. https://doi.org/10.1167/11.5.4
Braga, R. M., Wilson, L. R., Sharp, D. J., Wise, R. J. S., & Leech, R. (2013). Separable networks for top-down attention to auditory non-spatial and visuospatial modalities. *NeuroImage*, *74*, 77–86. https://doi.org/10.1016/j.neuroimage.2013.02.023
Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
Breska, A., & Deouell, L. Y. (2014). Automatic Bias of Temporal Expectations following Temporally Regular Input Independently of High-level Temporal Expectation. *Journal of Cognitive Neuroscience*, *26*(7), 1555–1571. https://doi.org/10.1162/jocn_a_00564
Breska, A., & Ivry, R. B. (2016). Taxonomies of timing: Where does the cerebellum fit in? *Current Opinion in Behavioral Sciences*, *8*, 282–288. https://doi.org/10.1016/j.cobeha.2016.02.034
Breska, A., & Ivry, R. B. (2018). Double dissociation of single-interval and rhythmic temporal prediction in cerebellar degeneration and Parkinson's disease. *Proceedings of the National Academy of Sciences*, *115*(48), 12283–12288. https://doi.org/10.1073/pnas.1810596115
Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews. Neuroscience*, *6*(10), 755–765. https://doi.org/10.1038/nrn1764
Buonomano, D., & Rovelli, C. (2021). *Bridging the neuroscience and physics of time.*
Buonomano, D. V., & Maass, W. (2009). State-dependent computations: Spatiotemporal processing in cortical networks. *Nature Reviews. Neuroscience*, *10*(2), 113–125. https://doi.org/10.1038/nrn2558
Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science (New York, N.Y.)*, *315*(5820), 1860–1862. https://doi.org/10.1126/science.1138071

Buzsáki, G. (2006). *Rhythms of the brain.* (pp. xv, 448). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195301069.001.0001
Cai, M., Stetson, C., & Eagleman, D. M. (2012). A neural model for temporal order judgments and their active recalibration: A common mechanism for space and time? *Frontiers in Psychology*, *3*, 470. https://doi.org/10.3389/fpsyg.2012.00470
Calderon, C. B., Gevers, W., & Verguts, T. (2018). The unfolding action model of initiation times, movement times, and movement paths. *Psychological Review*, *125*(5), 785–805. https://doi.org/10.1037/rev0000110
Capizzi, M., Correa, A., & Sanabria, D. (2013). Temporal orienting of attention is interfered by concurrent working memory updating. *Neuropsychologia*, *51*(2), 326–339. https://doi.org/10.1016/j.neuropsychologia.2012.10.005
Capizzi, M., Sanabria, D., & Correa, Á. (2012). Dissociating controlled from automatic processing in temporal preparation. *Cognition*, *123*(2), 293–302. https://doi.org/10.1016/j.cognition.2012.02.005
Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525. https://doi.org/10.1016/j.visres.2011.04.012
Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Research*, *40*(10–12), 1203–1215. https://doi.org/10.1016/s0042-6989(00)00024-9
Chalk, M., Seitz, A. R., & Series, P. (2010). Rapidly learned stimulus expectations alter perception of motion. *Journal of Vision*, *10*(8), 2–2. https://doi.org/10.1167/10.8.2
Chatham, C. H., & Badre, D. (2015). Multiple gates on working memory. *Current Opinion in Behavioral Sciences*, *1*, 23–31. https://doi.org/10.1016/j.cobeha.2014.08.001
Chatham, C. H., Frank, M. J., & Badre, D. (2014). Corticostriatal Output Gating during Selection from Working Memory. *Neuron*, *81*(4), 930–942. https://doi.org/10.1016/j.neuron.2014.01.002
Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*(6), 2918–2940. https://doi.org/10.1152/jn.1998.80.6.2918
Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *363*(6427), 345–347. https://doi.org/10.1038/363345a0
Cherry, E. C. (1953). Some experiments on the recognition of speech, with one and with two ears. *Journal of the Acoustical Society of America*, *25*, 975–979. https://doi.org/10.1121/1.1907229
Choi, I., Wang, L., Bharadwaj, H., & Shinn-Cunningham, B. (2014). Individual differences in attentional modulation of cortical responses correlate with selective attention performance. *Hearing Research*, *314*, 10–19. https://doi.org/10.1016/j.heares.2014.04.008
Chopin, A., & Mamassian, P. (2012). Predictive Properties of Visual Adaptation. *Current Biology*, *22*(7), 622–626. https://doi.org/10.1016/j.cub.2012.02.021
Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J.-D. (2018). Cortical specialization for attended versus unattended working memory. *Nature Neuroscience*, *21*(4), 494–496. https://doi.org/10.1038/s41593-018-0094-4
Chun, M. M. (2000). Contextual cueing of visual attention. *Trends in Cognitive Sciences*, *4*(5), 170–178. https://doi.org/10.1016/S1364-6613(00)01476-5
Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A Taxonomy of External and Internal Attention. *Annual Review of Psychology*, *62*(1), 73–101. https://doi.org/10.1146/annurev.psych.093008.100427

Chun, M. M., & Jiang, Y. (1998). Contextual Cueing: Implicit Learning and Memory of Visual Context Guides Spatial Attention. *Cognitive Psychology*, *36*(1), 28–71. https://doi.org/10.1006/cogp.1998.0681
Chun, M. M., & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nature Neuroscience*, *2*(9), 844–847. https://doi.org/10.1038/12222
Cicchini, G. M., Anobile, G., & Burr, D. C. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proceedings of the National Academy of Sciences*, *111*(21), 7867–7872. https://doi.org/10.1073/pnas.1402785111
Cicchini, G. M., Anobile, G., Chelli, E., Arrighi, R., & Burr, D. C. (2022). Uncertainty and Prior Assumptions, Rather Than Innate Logarithmic Encoding, Explain Nonlinear Number-to-Space Mapping. *Psychological Science*, *33*(1), 121–134. https://doi.org/10.1177/09567976211034501
Cicchini, G. M., Mikellidou, K., & Burr, D. C. (2018). The functional role of serial dependence. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1890), 20181722. https://doi.org/10.1098/rspb.2018.1722
Cicchini, G. M., Mikellidou, K., & Burr, D. C. (2024). Serial Dependence in Perception. *Annual Review of Psychology*, *75*(1), 129–154. https://doi.org/10.1146/annurev-psych-021523-104939
Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1485), 1585–1599. https://doi.org/10.1098/rstb.2007.2054
Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annual Review of Neuroscience*, *33*(1), 269–298. https://doi.org/10.1146/annurev.neuro.051508.135409
Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *The Behavioral and Brain Sciences*, *36*(3), 181–204. https://doi.org/10.1017/S0140525X12000477
Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2019). Electrical stimulation of alpha oscillations stabilizes performance on visual attention tasks. *Journal of Experimental Psychology. General*, *148*(2), 203–220. https://doi.org/10.1037/xge0000502
Clifford, C. W. G. (2002). Perceptual adaptation: Motion parallels orientation. *Trends in Cognitive Sciences*, *6*(3), 136–143. https://doi.org/10.1016/S1364-6613(00)01856-8
Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., & Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision Research*, *47*(25), 3125–3131. https://doi.org/10.1016/j.visres.2007.08.023
Cohen, M. R., & Maunsell, J. H. R. (2011). Using Neuronal Populations to Study the Mechanisms Underlying Spatial and Feature Attention. *Neuron*, *70*(6), 1192–1204. https://doi.org/10.1016/j.neuron.2011.04.029
Conditt, M. A., & Mussa-Ivaldi, F. A. (1999). Central representation of time during motor learning. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(20), 11625–11630. https://doi.org/10.1073/pnas.96.20.11625
Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., & Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*(4), 761–773. https://doi.org/10.1016/s0896-6273(00)80593-0
Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *The Journal of Neuroscience : The Official Journal of the Society for*

Neuroscience, *13*(3), 1202–1226. https://doi.org/10.1523/JNEUROSCI.13-03-01202.1993

Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science (New York, N.Y.)*, *270*(5237), 802–805. https://doi.org/10.1126/science.270.5237.802

Correa, Á. (2010). Enhancing behavioural performance by visual temporal orienting. In A. C. Nobre & J. T. Coull (Eds.), *Attention and Time* (1st ed., pp. 359–370). Oxford University PressOxford. https://doi.org/10.1093/acprof:oso/9780199563456.003.0026

Correa, A., Lupiáñez, J., & Tudela, P. (2005). Attentional preparation based on temporal expectancy modulates processing at the perceptual level. *Psychonomic Bulletin & Review*, *12*(2), 328–334. https://doi.org/10.3758/bf03196380

Correa, Lupiáñez, Madrid, & Tudela. (2006). Temporal attention enhances early visual processing: A review and new evidence from event-related potentials. *Brain Research*, *1076*(1), 116–128. https://doi.org/10.1016/j.brainres.2005.11.074

Correa, & Nobre. (2008). Neural modulation by regularity and passage of time. *Journal of Neurophysiology*, *100*(3), 1649–1655. https://doi.org/10.1152/jn.90656.2008

Cotti, J., Rohenkohl, G., Stokes, M., Nobre, A. C., & Coull, J. T. (2011). Functionally dissociating temporal and motor components of response preparation in left intraparietal sulcus. *NeuroImage*, *54*(2), 1221–1230. https://doi.org/10.1016/j.neuroimage.2010.09.038

Coull, Cheng, & Meck. (2011). Neuroanatomical and Neurochemical Substrates of Timing. *Neuropsychopharmacology*, *36*(1), Article 1. https://doi.org/10.1038/npp.2010.113

Coull, Frith, C. D., Büchel, C., & Nobre, A. C. (2000). Orienting attention in time: Behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia*, *38*(6), 808–819. https://doi.org/10.1016/s0028-3932(99)00132-3

Coull, J. T. (2004). fMRI studies of temporal attention: Allocating attention within, or towards, time. *Brain Research. Cognitive Brain Research*, *21*(2), 216–226. https://doi.org/10.1016/j.cogbrainres.2004.02.011

Coull, & Nobre. (1998). Where and When to Pay Attention: The Neural Systems for Directing Attention to Spatial Locations and to Time Intervals as Revealed by Both PET and fMRI. *The Journal of Neuroscience*, *18*(18), 7426–7435. https://doi.org/10.1523/JNEUROSCI.18-18-07426.1998

Coull, & Nobre. (2008). Dissociating explicit timing from temporal expectation with fMRI. *Current Opinion in Neurobiology*, *18*(2), 137–144. https://doi.org/10.1016/j.conb.2008.07.011

Coull, Nobre, & Frith. (2001). The Noradrenergic α2 Agonist Clonidine Modulates Behavioural and Neuroanatomical Correlates of Human Attentional Orienting and Alerting. *Cerebral Cortex*, *11*(1), 73–84. https://doi.org/10.1093/cercor/11.1.73

Covington, N. V., Brown-Schmidt, S., & Duff, M. C. (2018). The Necessity of the Hippocampus for Statistical Learning. *Journal of Cognitive Neuroscience*, *30*(5), 680–697. https://doi.org/10.1162/jocn_a_01228

Cravo, A. M., Rohenkohl, G., Santos, K. M., & Nobre, A. C. (2017). Temporal Anticipation Based on Memory. *Journal of Cognitive Neuroscience*, *29*(12), 2081–2089. https://doi.org/10.1162/jocn_a_01172

Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2013). Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *33*(9), 4002–4010. https://doi.org/10.1523/JNEUROSCI.4675-12.2013

Cristescu, T. C., Devlin, J. T., & Nobre, A. C. (2006). Orienting attention to semantic categories. *NeuroImage*, *33*(4), 1178–1187. https://doi.org/10.1016/j.neuroimage.2006.08.017
Cristescu, T. C., & Nobre, A. C. (2008). Differential modulation of word recognition by semantic and spatial orienting of attention. *Journal of Cognitive Neuroscience*, *20*(5), 787–801. https://doi.org/10.1162/jocn.2008.20503
Czoschke, S., Fischer, C., Beitner, J., Kaiser, J., & Bledowski, C. (2019). Two types of serial dependence in visual working memory. *British Journal of Psychology*, *110*(2), 256–267. https://doi.org/10.1111/bjop.12349
Davranche, K., Nazarian, B., Vidal, F., & Coull, J. (2011). Orienting Attention in Time Activates Left Intraparietal Sulcus for Both Perceptual and Motor Task Goals. *Journal of Cognitive Neuroscience*, *23*(11), 3318–3330. https://doi.org/10.1162/jocn_a_00030
de la Rosa, M. D., Sanabria, D., Capizzi, M., & Correa, A. (2012). Temporal Preparation Driven by Rhythms is Resistant to Working Memory Interference. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00308
de Lange, F. P., Heilbron, M., & Kok, P. (2018). How Do Expectations Shape Perception? *Trends in Cognitive Sciences*, *22*(9), 764–779. https://doi.org/10.1016/j.tics.2018.06.002
de Vries, E., & van Ede, F. (2024). Microsaccades Track Location-Based Object Rehearsal in Visual Working Memory. *eNeuro*, *11*(1), ENEURO.0276-23.2023. https://doi.org/10.1523/ENEURO.0276-23.2023
de Vries, I. E. J., Savran, E., van Driel, J., & Olivers, C. N. L. (2019). Oscillatory Mechanisms of Preparing for Visual Distraction. *Journal of Cognitive Neuroscience*, *31*(12), 1873–1894. https://doi.org/10.1162/jocn_a_01460
De Vries, I. E. J., Slagter, H. A., & Olivers, C. N. L. (2020). Oscillatory Control over Representational States in Working Memory. *Trends in Cognitive Sciences*, *24*(2), 150–162. https://doi.org/10.1016/j.tics.2019.11.006
De Vries, I. E. J., Van Driel, J., Karacaoglu, M., & Olivers, C. N. L. (2018). Priority Switches in Visual Working Memory are Supported by Frontal Delta and Posterior Alpha Interactions. *Cerebral Cortex*, *28*(11), 4090–4104. https://doi.org/10.1093/cercor/bhy223
De Vries, I. E. J., Van Driel, J., & Olivers, C. N. L. (2017). Posterior α EEG Dynamics Dissociate Current from Future Goals in Working Memory-Guided Visual Search. *The Journal of Neuroscience*, *37*(6), 1591–1603. https://doi.org/10.1523/JNEUROSCI.2945-16.2016
Demarchi, G., Sanchez, G., & Weisz, N. (2019). Automatic and feature-specific prediction-related neural activity in the human auditory system. *Nature Communications*, *10*(1), 3440. https://doi.org/10.1038/s41467-019-11440-1
Denison, R. N., Carrasco, M., & Heeger, D. J. (2021). A dynamic normalization model of temporal attention. *Nature Human Behaviour*, *5*(12), 1674–1685. https://doi.org/10.1038/s41562-021-01129-1
Denison, R. N., Heeger, D. J., & Carrasco, M. (2017). Attention flexibly trades off across points in time. *Psychonomic Bulletin & Review*, *24*(4), 1142–1151. https://doi.org/10.3758/s13423-016-1216-1
Denison, R. N., Parker, J. A., & Carrasco, M. (2020). Modeling pupil responses to rapid sequential events. *Behavior Research Methods*, *52*(5), 1991–2007. https://doi.org/10.3758/s13428-020-01368-6
Denison, R. N., Yuval-Greenberg, S., & Carrasco, M. (2019). Directing Voluntary Temporal Attention Increases Fixational Stability. *The Journal of Neuroscience*, *39*(2), 353–363. https://doi.org/10.1523/JNEUROSCI.1926-18.2018

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222. https://doi.org/10.1146/annurev.ne.18.030195.001205

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4

Ding, N., & Simon, J. Z. (2012). Emergence of neural encoding of auditory objects while listening to competing speakers. *Proceedings of the National Academy of Sciences*, *109*(29), 11854–11859. https://doi.org/10.1073/pnas.1205381109

Doherty, Rao, A, Mesulam, MM, & Nobre, AC. (2005). Synergistic Effect of Combined Temporal and Spatial Expectations on Visual Attention. *Journal of Neuroscience*, *25*(36), 8259–8266. https://doi.org/10.1523/JNEUROSCI.1821-05.2005

Dong, D. W., & Atick, J. J. (1995). STATISTICS OF NATURAL TIME-VARYING IMAGES. *Network: Computation In Neural Systems*, *6*, 345–358.

Draschkow, D., Nobre, A. C., & Van Ede, F. (2022). Multiple spatial frames for immersive working memory. *Nature Human Behaviour*, *6*(4), 536–544. https://doi.org/10.1038/s41562-021-01245-y

Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*(1–2), 39–88. https://doi.org/10.1016/s0010-0277(00)00124-4

Duyar, A., Denison, R. N., & Carrasco, M. (2023). Exogenous temporal attention varies with temporal uncertainty. *Journal of Vision*, *23*(3), 9. https://doi.org/10.1167/jov.23.3.9

Echeverria-Altuna, I., Quinn, A. J., Zokaei, N., Woolrich, M. W., Nobre, A. C., & Van Ede, F. (2022). Transient beta activity and cortico-muscular connectivity during sustained motor behaviour. *Progress in Neurobiology*, *214*, 102281. https://doi.org/10.1016/j.pneurobio.2022.102281

Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*(11), 732–744. https://doi.org/10.1038/nrn3827

Eimer, M. (1998). Mechanisms of Visuospatial Attention: Evidence from Event-related Brain Potentials. *Visual Cognition*, *5*(1–2), 257–286. https://doi.org/10.1080/713756778

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Ester, E., & Weese, R. (2023). Temporally Dissociable Mechanisms of Spatial, Feature, and Motor Selection during Working Memory–guided Behavior. *Journal of Cognitive Neuroscience*, *35*(12), 2014–2027. https://doi.org/10.1162/jocn_a_02061

Esterman, M., Chiu, Y.-C., Tamber-Rosenau, B. J., & Yantis, S. (2009). Decoding cognitive control in human parietal cortex. *Proceedings of the National Academy of Sciences*, *106*(42), 17974–17979. https://doi.org/10.1073/pnas.0903593106

Fahle, M., & Poggio, T. (2002). *Perceptual learning.* (pp. xx, 455). MIT Press.

Fan, Y. (范莹), Han, Q. (韩起明), Guo, S. (郭思萌), & Luo, H. (罗欢). (2021). Distinct Neural Representations of Content and Ordinal Structure in Auditory Sequence Memory. *The Journal of Neuroscience*, *41*(29), 6290. https://doi.org/10.1523/JNEUROSCI.0320-21.2021

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/bf03193146

Feingold, J., Gibson, D. J., DePasquale, B., & Graybiel, A. M. (2015). Bursts of beta oscillation differentiate postperformance activity in the striatum and motor cortex of monkeys performing movement tasks. *Proceedings of the National Academy of Sciences of*

the United States of America, *112*(44), 13687–13692. https://doi.org/10.1073/pnas.1517629112
Felsen, G., Touryan, J., Han, F., & Dan, Y. (2005). Cortical Sensitivity to Visual Features in Natural Scenes. *PLoS Biology*, *3*(10), e342. https://doi.org/10.1371/journal.pbio.0030342
Fernández, A., Denison, R. N., & Carrasco, M. (2019). Temporal attention improves perception similarly at foveal and parafoveal locations. *Journal of Vision*, *19*(1), 12. https://doi.org/10.1167/19.1.12
Fernberger, S. W. (1920). Interdependence of judgments within the series for the method of constant stimuli. *Journal of Experimental Psychology*, *3*(2), 126.
Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron*, *99*(4), 842-853.e8. https://doi.org/10.1016/j.neuron.2018.07.038
Firestone, C., & Scholl, B. J. (2014). "Top-down" effects where none should be found: The El Greco fallacy in perception research. *Psychological Science*, *25*(1), 38–46. https://doi.org/10.1177/0956797613485092
Firestone, C., & Scholl, B. J. (2016). Cognition does not affect perception: Evaluating the evidence for 'top-down' effects. *The Behavioral and Brain Sciences*, *39*, e229. https://doi.org/10.1017/S0140525X15000965
Fischer, C., Czoschke, S., Peters, B., Rahm, B., Kaiser, J., & Bledowski, C. (2020). Context information supports serial dependence of multiple visual objects across memory episodes. *Nature Communications*, *11*(1), 1932. https://doi.org/10.1038/s41467-020-15874-w
Fischer, & Whitney. (2014). Serial dependence in visual perception. *Nature Neuroscience*, *17*(5), 738–743. https://doi.org/10.1038/nn.3689
Fiser, J., & Lengyel, G. (2022). Statistical Learning in Vision. *Annual Review of Vision Science*, *8*(1), 265–290. https://doi.org/10.1146/annurev-vision-100720-103343
Formica, S., González-García, C., Senoussi, M., & Brass, M. (2021). Neural oscillations track the maintenance and proceduralization of novel instructions. *NeuroImage*, *232*, 117870. https://doi.org/10.1016/j.neuroimage.2021.117870
Forte, A. E., Etard, O., & Reichenbach, T. (2017). The human auditory brainstem response to running speech reveals a subcortical mechanism for selective attention. *eLife*, *6*, e27203. https://doi.org/10.7554/eLife.27203
Foster, J. J., Sutterer, D. W., Serences, J. T., Vogel, E. K., & Awh, E. (2017). Alpha-Band Oscillations Enable Spatially and Temporally Resolved Tracking of Covert Spatial Attention. *Psychological Science*, *28*(7), 929–941. https://doi.org/10.1177/0956797617699167
Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport*, *9*(17), 3929–3933. https://doi.org/10.1097/00001756-199812010-00030
Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480. https://doi.org/10.1016/j.tics.2005.08.011
Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science (New York, N.Y.)*, *291*(5508), 1560–1563. https://doi.org/10.1126/science.1055465
Fries, P., Womelsdorf, T., Oostenveld, R., & Desimone, R. (2008). The Effects of Visual Stimulation and Selective Visual Attention on Rhythmic Neuronal Synchronization in Macaque Area V4. *The Journal of Neuroscience*, *28*(18), 4823. https://doi.org/10.1523/JNEUROSCI.4499-07.2008

Fritsche, M., Solomon, S. G., & De Lange, F. P. (2022). Brief Stimuli Cast a Persistent Long-Term Trace in Visual Cortex. *The Journal of Neuroscience*, *42*(10), 1999–2010. https://doi.org/10.1523/JNEUROSCI.1350-21.2021

Fritsche, M., Spaak, E., & De Lange, F. P. (2020). A Bayesian and efficient observer model explains concurrent attractive and repulsive history biases in visual perception. *eLife*, *9*, e55389. https://doi.org/10.7554/eLife.55389

Fukuda, K., Kang, M.-S., & Woodman, G. F. (2016). Distinct neural mechanisms for spatially lateralized and spatially global visual working memory representations. *Journal of Neurophysiology*, *116*(4), 1715–1727. https://doi.org/10.1152/jn.00991.2015

Fukuda, K., Mance, I., & Vogel, E. K. (2015). α Power Modulation and Event-Related Slow Wave Provide Dissociable Correlates of Visual Working Memory. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(41), 14009–14016. https://doi.org/10.1523/JNEUROSCI.5003-14.2015

Fuster, J. M., & Bressler, S. L. (2012). Cognit activation: A mechanism enabling temporal integration in working memory. *Trends in Cognitive Sciences*, *16*(4), 207–218. https://doi.org/10.1016/j.tics.2012.03.005

Gabay, S., & Henik, A. (2010). Temporal expectancy modulates inhibition of return in a discrimination task. *Psychonomic Bulletin & Review*, *17*(1), 47–51. https://doi.org/10.3758/PBR.17.1.47

Galbraith, G. C., & Arroyo, C. (1993). Selective attention and brainstem frequency-following responses. *Biological Psychology*, *37*(1), 3–22. https://doi.org/10.1016/0301-0511(93)90024-3

Gallivan, J. P., Barton, K. S., Chapman, C. S., Wolpert, D. M., & Randall Flanagan, J. (2015). Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nature Communications*, *6*(1), 7428. https://doi.org/10.1038/ncomms8428

Gallivan, J. P., Logan, L., Wolpert, D. M., & Flanagan, J. R. (2016). Parallel specification of competing sensorimotor control policies for alternative action options. *Nature Neuroscience*, *19*(2), 320–326. https://doi.org/10.1038/nn.4214

Galluzzi, F., Benedetto, A., Cicchini, G. M., & Burr, D. C. (2022). Visual priming and serial dependence are mediated by separate mechanisms. *Journal of Vision*, *22*(10), 1. https://doi.org/10.1167/jov.22.10.1

Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences*, *96*(6), 3314–3319. https://doi.org/10.1073/pnas.96.6.3314

Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: Bridging selective attention and working memory. *Trends in Cognitive Sciences*, *16*(2), 129–135. https://doi.org/10.1016/j.tics.2011.11.014

Gekas, N., Chalk, M., Seitz, A. R., & Seriès, P. (2013). Complexity and specificity of experimentally-induced expectations in motion perception. *Journal of Vision*, *13*(4), 8–8. https://doi.org/10.1167/13.4.8

Gekas, N., McDermott, K. C., & Mamassian, P. (2019). Disambiguating serial effects of multiple timescales. *Journal of Vision*, *19*(6), 24. https://doi.org/10.1167/19.6.24

Gekas, N., Seitz, A. R., & Seriès, P. (2015). Expectations developed over multiple timescales facilitate visual search performance. *Journal of Vision*, *15*(9), 10. https://doi.org/10.1167/15.9.10

Geng, J. J. (2014). Attentional Mechanisms of Distractor Suppression. *Current Directions in Psychological Science*, *23*(2), 147–153. https://doi.org/10.1177/0963721414525780

Ghose, G. M., & Bearl, D. W. (2010). Attention directed by expectations enhances receptive fields in cortical area MT. *Vision Research*, *50*(4), 441–451. https://doi.org/10.1016/j.visres.2009.10.003

Ghose, G. M., & Maunsell, J. H. R. (2002). Attentional modulation in visual cortex depends on task timing. *Nature*, *419*(6907), 616–620. https://doi.org/10.1038/nature01057

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of Sciences*, *423*, 52–77. https://doi.org/10.1111/j.1749-6632.1984.tb23417.x

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*(5), 453–467. https://doi.org/10.1037/h0059826

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*(5), 350–363. https://doi.org/10.1038/nrn3476

Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: Visual orientation perception reflects knowledge of environmental statistics. *Nature Neuroscience*, *14*(7), 926–932. https://doi.org/10.1038/nn.2831

Glasauer, S., & Shi, Z. (2022). Individual beliefs about temporal continuity explain variation of perceptual biases. *Scientific Reports*, *12*(1), 10746. https://doi.org/10.1038/s41598-022-14939-8

Goldberg, M. E., & Bushnell, M. C. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *Journal of Neurophysiology*, *46*(4), 773–787. https://doi.org/10.1152/jn.1981.46.4.773

Goldfarb, E. V., Chun, M. M., & Phelps, E. A. (2016). Memory-Guided Attention: Independent Contributions of the Hippocampus and Striatum. *Neuron*, *89*(2), 317–324. https://doi.org/10.1016/j.neuron.2015.12.014

González-García, C., Formica, S., Liefooghe, B., & Brass, M. (2020). Attentional prioritization reconfigures novel instructions into action-oriented task sets. *Cognition*, *194*, 104059. https://doi.org/10.1016/j.cognition.2019.104059

Gramfort, A. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience*, *7*. https://doi.org/10.3389/fnins.2013.00267

Gregoriou, G. G., Gotts, S. J., & Desimone, R. (2012). Cell-Type-Specific Synchronization of Neural Activity in FEF with V4 during Attention. *Neuron*, *73*(3), 581–594. https://doi.org/10.1016/j.neuron.2011.12.019

Gresch, D., Boettcher, S. E. P., Van Ede, F., & Nobre, A. C. (2021). Shielding working-memory representations from temporally predictable external interference. *Cognition*, *217*, 104915. https://doi.org/10.1016/j.cognition.2021.104915

Gresch, D., Boettcher, S. E. P., Van Ede, F., & Nobre, A. C. (2024). Shifting attention between perception and working memory. *Cognition*, *245*, 105731. https://doi.org/10.1016/j.cognition.2024.105731

Griffin, I. C., & Nobre, A. C. (2003). Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. https://doi.org/10.1162/089892903322598139

Griffin, Miniussi, & Nobre. (2001). ORIENTING ATTENTION IN TIME. *Frontiers in Bioscience*, *6*, 660–671.

Griffin, Miniussi, & Nobre. (2002). Multiple mechanisms of selective attention: Differential modulation of stimulus processing by attention to space or time. *Neuropsychologia*, *40*(13), 2325–2340. https://doi.org/10.1016/S0028-3932(02)00087-8

Grubert, A., & Eimer, M. (2018). The Time Course of Target Template Activation Processes during Preparation for Visual Search. *The Journal of Neuroscience*, *38*(44), 9527. https://doi.org/10.1523/JNEUROSCI.0409-18.2018

Hahn, M., & Wei, X.-X. (2024). A unifying theory explains seemingly contradictory biases in perceptual estimation. *Nature Neuroscience*. https://doi.org/10.1038/s41593-024-01574-x

Hajonides, J. E., Van Ede, F., Stokes, M. G., Nobre, A. C., & Myers, N. E. (2023). Multiple and Dissociable Effects of Sensory History on Working-Memory Performance. *The Journal of Neuroscience*, *43*(15), 2730–2740. https://doi.org/10.1523/JNEUROSCI.1200-22.2023

Hari, R., & Salmelin, R. (1997). Human cortical oscillations: A neuromagnetic view through the skull. *Trends in Neurosciences*, *20*(1), 44–49. https://doi.org/10.1016/S0166-2236(96)10065-5

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635. https://doi.org/10.1038/nature07832

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J., & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(4), 802–811. https://doi.org/10.1037//0096-1523.16.4.802

Heideman, S. G., Quinn, A. J., Woolrich, M. W., van Ede, F., & Nobre, A. C. (2020). Dissecting beta-state changes during timed movement preparation in Parkinson's disease. *Progress in Neurobiology*, *184*, 101731. https://doi.org/10.1016/j.pneurobio.2019.101731

Heideman, S. G., Rohenkohl, G., Chauvin, J. J., Palmer, C. E., van Ede, F., & Nobre, A. C. (2018). Anticipatory neural dynamics of spatial-temporal orienting of attention in younger and older adults. *NeuroImage*, *178*, 46–56. https://doi.org/10.1016/j.neuroimage.2018.05.002

Heideman, S. G., van Ede, F., & Nobre, A. C. (2018a). Early Behavioural Facilitation by Temporal Expectations in Complex Visual-motor Sequences. *Neuroscience*, *389*, 74–84. https://doi.org/10.1016/j.neuroscience.2018.05.014

Heideman, S. G., van Ede, F., & Nobre, A. C. (2018b). Temporal alignment of anticipatory motor cortical beta lateralisation in hidden visual-motor sequences. *European Journal of Neuroscience*, *48*(8), 2684–2695. https://doi.org/10.1111/ejn.13700

Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, *30*(3), 327–330. https://doi.org/10.1212/wnl.30.3.327

Heinen, S. J., & Liu, M. (1997). Single-neuron activity in the dorsomedial frontal cortex during smooth-pursuit eye movements to predictable target motion. *Visual Neuroscience*, *14*(5), 853–865. Cambridge Core. https://doi.org/10.1017/S0952523800011597

Henderson, M. M., Rademaker, R. L., & Serences, J. T. (2022). Flexible utilization of spatial- and motor-based codes for the storage of visuo-spatial information. *eLife*, *11*, e75688. https://doi.org/10.7554/eLife.75688

Heuer, A., Ohl, S., & Rolfs, M. (2020). Memory for action: A functional view of selection in visual working memory. *Visual Cognition*, *28*(5–8), 388–400. https://doi.org/10.1080/13506285.2020.1764156

Higo, T., Mars, R. B., Boorman, E. D., Buch, E. R., & Rushworth, M. F. S. (2011). Distributed and causal influence of frontal operculum in task control. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(10), 4230–4235. https://doi.org/10.1073/pnas.1013361108

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 781–787. https://doi.org/10.1073/pnas.95.3.781

Hillyard, S. A., Hink, R. F., Schwent, V. L., & Picton, T. W. (1973). Electrical signs of selective attention in the human brain. *Science (New York, N.Y.)*, *182*(4108), 177–180. https://doi.org/10.1126/science.182.4108.177

Hollingworth, H. L. (1910). The Central Tendency of Judgment. *The Journal of Philosophy, Psychology and Scientific Methods*, *7*(17), 461–469.
Hopf, J.-M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H.-J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *24*(8), 1822–1832. https://doi.org/10.1523/JNEUROSCI.3564-03.2004
Husain, M., & Rorden, C. (2003). Non-spatially lateralized mechanisms in hemispatial neglect. *Nature Reviews. Neuroscience*, *4*(1), 26–36. https://doi.org/10.1038/nrn1005
Hutchinson, J. B., & Turk-Browne, N. B. (2012). Memory-guided attention: Control from multiple memory systems. *Trends in Cognitive Sciences*, *16*(12), 576–579. https://doi.org/10.1016/j.tics.2012.10.003
Huttenlocher, J., Hedges, L. V., & Vevea, J. L. (2000). Why Do Categories Affect Stimulus Judgment? *Journal of Experimental Psychology: General*, *129*(2), 220–241.
Iemi, L., Gwilliams, L., Samaha, J., Auksztulewicz, R., Cycowicz, Y. M., King, J.-R., Nikulin, V. V., Thesen, T., Doyle, W., Devinsky, O., Schroeder, C. E., Melloni, L., & Haegens, S. (2022). Ongoing neural oscillations influence behavior and sensory representations by suppressing neuronal excitability. *NeuroImage*, *247*, 118746. https://doi.org/10.1016/j.neuroimage.2021.118746
Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience*, *1*(2), 136–152. https://doi.org/10.1162/jocn.1989.1.2.136
Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, *12*(7), 273–280. https://doi.org/10.1016/j.tics.2008.04.002
Ivry, R. B., & Spencer, R. M. C. (2004). The neural representation of time. *Current Opinion in Neurobiology*, *14*(2), 225–232. https://doi.org/10.1016/j.conb.2004.03.013
Ivry, R. B., Spencer, R. M., Zelaznik, H. N., & Diedrichsen, J. (2002). The cerebellum and event timing. *Annals of the New York Academy of Sciences*, *978*, 302–317. https://doi.org/10.1111/j.1749-6632.2002.tb07576.x
Janssen, P., & Shadlen, M. N. (2005). A representation of the hazard rate of elapsed time in macaque area LIP. *Nature Neuroscience*, *8*(2), 234–241. https://doi.org/10.1038/nn1386
Jaramillo, S., & Zador, A. M. (2011). The auditory cortex mediates the perceptual effects of acoustic temporal expectation. *Nature Neuroscience*, *14*(2), 246–251. https://doi.org/10.1038/nn.2688
Jasper, H., & Penfield, W. (1949). Electrocorticograms in man: Effect of voluntary movement upon the electrical activity of the precentral gyrus. *Archiv Für Psychiatrie Und Nervenkrankheiten*, *183*(1), 163–174. https://doi.org/10.1007/BF01062488
Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, *13*(8), 1020–1026. https://doi.org/10.1038/nn.2590
Jenkinson, N., & Brown, P. (2011). New insights into the relationship between dopamine, beta oscillations and motor function. *Trends in Neurosciences*, *34*(12), Article 12. https://doi.org/10.1016/j.tins.2011.09.003
Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00186
Jepma, M., Wagenmakers, E.-J., & Nieuwenhuis, S. (2012). Temporal expectation and information processing: A model-based analysis. *Cognition*, *122*(3), 426–441. https://doi.org/10.1016/j.cognition.2011.11.014
Jiang, J., Summerfield, C., & Egner, T. (2013). Attention sharpens the distinction between expected and unexpected percepts in the visual brain. *The Journal of Neuroscience : The*

Official Journal of the Society for Neuroscience, *33*(47), 18438–18447. https://doi.org/10.1523/JNEUROSCI.3308-13.2013

Jin, W., Nobre, A. C., & van Ede, F. (2020). Temporal Expectations Prepare Visual Working Memory for Behavior. *Journal of Cognitive Neuroscience*, *32*(12), 2320–2332. https://doi.org/10.1162/jocn_a_01626

Jones, M. R. (1976). Time, our lost dimension: Toward a new theory of perception, attention, and memory. *Psychological Review*, *83*(5), 323–355.

Jones, M. R., Moynihan, H., MacKenzie, N., & Puente, J. (2002). Temporal aspects of stimulus-driven attending in dynamic arrays. *Psychological Science*, *13*(4), 313–319. https://doi.org/10.1111/1467-9280.00458

Jones, S. R. (2016). When brain rhythms aren't 'rhythmic': Implication for their mechanisms and meaning. *Current Opinion in Neurobiology*, *40*, 72–80. https://doi.org/10.1016/j.conb.2016.06.010

Kaiser, J., Birbaumer, N., & Lutzenberger, W. (2001). Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neuroscience Letters*, *312*(3), 149–152. https://doi.org/10.1016/S0304-3940(01)02217-0

Kalm, K., & Norris, D. (2018). Visual recency bias is explained by a mixture model of internal representations. *Journal of Vision*, *18*(7), 1. https://doi.org/10.1167/18.7.1

Karmarkar, U. R., & Buonomano, D. V. (2007). Timing in the absence of clocks: Encoding time in neural network states. *Neuron*, *53*(3), 427–438. https://doi.org/10.1016/j.neuron.2007.01.006

Karnath, H., Himmelbach, M., & Rorden, C. (2002). The subcortical anatomy of human spatial neglect: Putamen, caudate nucleus and pulvinar. *Brain*, *125*(2), 350–360. https://doi.org/10.1093/brain/awf032

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*(4), 751–761. https://doi.org/10.1016/s0896-6273(00)80734-5

Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*(12), 1263–1276. https://doi.org/10.1016/s0028-3932(01)00116-6

Kikumoto, A., Mayr, U., & Badre, D. (2022). The role of conjunctive representations in prioritizing and selecting planned actions. *eLife*, *11*, e80153. https://doi.org/10.7554/eLife.80153

Kilavik, B. E., & Riehle, A. (2010). Timing structures' neuronal activity during preparation for action. In A. C. Nobre & J. T. Coull (Eds.), *Attention and Time* (1st ed., pp. 257–272). Oxford University PressOxford. https://doi.org/10.1093/acprof:oso/9780199563456.003.0019

Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups and downs of β oscillations in sensorimotor cortex. *Experimental Neurology*, *245*, 15–26. https://doi.org/10.1016/j.expneurol.2012.09.014

Kingstone, A. (1992). Combining Expectancies. *The Quarterly Journal of Experimental Psychology Section A*, *44*(1), 69–104. https://doi.org/10.1080/14640749208401284

Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologica*, *33*, 193–201. https://doi.org/10.1016/0001-6918(70)90132-0

Kiyonaga, A., Scimeca, J. M., Bliss, D. P., & Whitney, D. (2017). Serial Dependence across Perception, Attention, and Memory. *Trends in Cognitive Sciences*, *21*(7), 493–497. https://doi.org/10.1016/j.tics.2017.04.011

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007
Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003
Klostermann, F., Nikulin, V. V., Kühn, A. A., Marzinzik, F., Wahl, M., Pogosyan, A., Kupsch, A., Schneider, G.-H., Brown, P., & Curio, G. (2007). Task-related differential dynamics of EEG alpha- and beta-band synchronization in cortico-basal motor structures. *European Journal of Neuroscience*, *25*(5), 1604–1615. https://doi.org/10.1111/j.1460-9568.2007.05417.x
Kohn, A. (2007). Visual Adaptation: Physiology, Mechanisms, and Functional Benefits. *Journal of Neurophysiology*, *97*(5), 3155–3164. https://doi.org/10.1152/jn.00086.2007
Kok, P., Brouwer, G. J., Van Gerven, M. A. J., & De Lange, F. P. (2013). Prior Expectations Bias Sensory Representations in Visual Cortex. *The Journal of Neuroscience*, *33*(41), 16275–16284. https://doi.org/10.1523/JNEUROSCI.0742-13.2013
Kok, P., Jehee, J. F. M., & de Lange, F. P. (2012). Less Is More: Expectation Sharpens Representations in the Primary Visual Cortex. *Neuron*, *75*(2), 265–270. https://doi.org/10.1016/j.neuron.2012.04.034
Kok, P., Mostert, P., & de Lange, F. P. (2017). Prior expectations induce prestimulus sensory templates. *Proceedings of the National Academy of Sciences*, *114*(39), 10473–10478. https://doi.org/10.1073/pnas.1705652114
Kornysheva, K. (2016). Encoding Temporal Features of Skilled Movements—What, Whether and How? In J. Laczko & M. L. Latash (Eds.), *Progress in Motor Control* (Vol. 957, pp. 35–54). Springer International Publishing. https://doi.org/10.1007/978-3-319-47313-0_3
Kornysheva, K., & Diedrichsen, J. (2014). Human premotor areas parse sequences into their spatial and temporal features. *eLife*, *3*, e03043. https://doi.org/10.7554/eLife.03043
Kornysheva, K., Sierk, A., & Diedrichsen, J. (2013). Interaction of temporal and ordinal representations in movement sequences. *Journal of Neurophysiology*, *109*(5), 1416–1424. https://doi.org/10.1152/jn.00509.2012
Kuo, B.-C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for Targets within the Spatial Layout of Visual Short-Term Memory. *Journal of Neuroscience*, *29*(25), 8032–8038. https://doi.org/10.1523/JNEUROSCI.0952-09.2009
Kuo, B.-C., Stokes, M. G., Murray, A. M., & Nobre, A. C. (2014). Attention Biases Visual Activity in Visual Short-term Memory. *Journal of Cognitive Neuroscience*, *26*(7), 1377–1389. https://doi.org/10.1162/jocn_a_00577
Lakatos, P., Chen, C.-M., O'Connell, M. N., Mills, A., & Schroeder, C. E. (2007). Neuronal oscillations and multisensory interaction in primary auditory cortex. *Neuron*, *53*(2), 279–292. https://doi.org/10.1016/j.neuron.2006.12.011
Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science (New York, N.Y.)*, *320*(5872), 110–113. https://doi.org/10.1126/science.1154735
Lakatos, P., Musacchia, G., O'Connel, M. N., Falchier, A. Y., Javitt, D. C., & Schroeder, C. E. (2013). The spectrotemporal filter mechanism of auditory selective attention. *Neuron*, *77*(4), 750–761. https://doi.org/10.1016/j.neuron.2012.11.034
Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, *43*(2), 149–164. https://doi.org/10.1016/S0042-6989(02)00402-9

Lange, K., Krämer, U. M., & Röder, B. (2006). Attending points in time and space. *Experimental Brain Research*, *173*(1), 130–140. https://doi.org/10.1007/s00221-006-0372-3

Lange, K., & Röder, B. (2010). Temporal orienting in audition, touch, and across modalities. In A. C. Nobre & J. T. Coull (Eds.), *Attention and Time* (1st ed., pp. 393–406). Oxford University PressOxford. https://doi.org/10.1093/acprof:oso/9780199563456.003.0028

Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track time-varying events. *Psychological Review*, *106*(1), 119–159. https://doi.org/10.1037/0033-295X.106.1.119

LaRocque, J. J., Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding Attended Information in Short-term Memory: An EEG Study. *Journal of Cognitive Neuroscience*, *25*(1), 127–142. https://doi.org/10.1162/jocn_a_00305

Lashley, K. S. (1951). The problem of serial order in behavior. In *Cerebral mechanisms in behavior; the Hixon Symposium.* (pp. 112–146). Wiley.

Lee, A. K. C., Larson, E., Maddox, R. K., & Shinn-Cunningham, B. G. (2014). Using neuroimaging to understand the cortical mechanisms of auditory selective attention. *Hearing Research*, *307*, 111–120. https://doi.org/10.1016/j.heares.2013.06.010

Lee, A. K. C., Rajaram, S., Xia, J., Bharadwaj, H., Larson, E., Hämäläinen, M. S., & Shinn-Cunningham, B. G. (2012). Auditory selective attention reveals preparatory activity in different cortical regions for selection based on source location and source pitch. *Frontiers in Neuroscience*, *6*, 190. https://doi.org/10.3389/fnins.2012.00190

Leocani, L., Toro, C., Manganotti, P., Zhuang, P., & Hallett, M. (1997). Event-related coherence and event-related desynchronization/synchronization in the 10 Hz and 20 Hz EEG during self-paced movements. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *104*(3), 199–206. https://doi.org/10.1016/S0168-5597(96)96051-7

Lepsien, J., Griffin, I. C., Devlin, J. T., & Nobre, A. C. (2005). Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load. *NeuroImage*, *26*(3), 733–743. https://doi.org/10.1016/j.neuroimage.2005.02.026

Lepsien, J., & Nobre, A. C. (2007). Attentional Modulation of Object Representations in Working Memory. *Cerebral Cortex*, *17*(9), 2072–2083. https://doi.org/10.1093/cercor/bhl116

Lepsien, J., Thornton, I., & Nobre, A. C. (2011). Modulation of working-memory maintenance by directed attention. *Neuropsychologia*, *49*(6), 1569–1577. https://doi.org/10.1016/j.neuropsychologia.2011.03.011

Levitin, D. J., & Rogers, S. E. (2005). Absolute pitch: Perception, coding, and controversies. *Trends in Cognitive Sciences*, *9*(1), 26–33. https://doi.org/10.1016/j.tics.2004.11.007

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the Acoustical Society of America*, *49*(2), Suppl 2:467+.

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural Evidence for a Distinction between Short-term Memory and the Focus of Attention. *Journal of Cognitive Neuroscience*, *24*(1), 61–79. https://doi.org/10.1162/jocn_a_00140

Li, Q., Joo, S. J., Yeatman, J. D., & Reinecke, K. (2020). Controlling for Participants' Viewing Distance in Large-Scale, Psychophysical Online Experiments Using a Virtual Chinrest. *Scientific Reports*, *10*(1), 904. https://doi.org/10.1038/s41598-019-57204-1

Liberman, A., Fischer, J., & Whitney, D. (2014). Serial dependence in the perception of faces. *Current Biology : CB*, *24*(21), 2569–2574. https://doi.org/10.1016/j.cub.2014.09.025

Lieder, I., Adam, V., Frenkel, O., Jaffe-Dax, S., Sahani, M., & Ahissar, M. (2019). Perceptual bias reveals slow-updating in autism and fast-forgetting in dyslexia. *Nature Neuroscience*, *22*(2), 256–264. https://doi.org/10.1038/s41593-018-0308-9

Lim, S.-J., Wöstmann, M., & Obleser, J. (2015). Selective Attention to Auditory Memory Neurally Enhances Perceptual Precision. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *35*(49), 16094–16104. https://doi.org/10.1523/JNEUROSCI.2674-15.2015

Lima, B., Singer, W., & Neuenschwander, S. (2011). Gamma Responses Correlate with Temporal Expectation in Monkey Primary Visual Cortex. *The Journal of Neuroscience*, *31*(44), 15919–15931. https://doi.org/10.1523/JNEUROSCI.0957-11.2011

Liu, B., Nobre, A. C., & Van Ede, F. (2022). Functional but not obligatory link between microsaccades and neural modulation by covert spatial attention. *Nature Communications*, *13*(1), 3503. https://doi.org/10.1038/s41467-022-31217-3

Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, *47*(1), 108–113. https://doi.org/10.1016/j.visres.2006.09.017

Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01171

Los, S. A. (2004). Inhibition of return and nonspecific preparation: Separable inhibitory control mechanisms in space and time. *Perception & Psychophysics*, *66*(1), 119–130. https://doi.org/10.3758/BF03194866

Los, S. A. (2010). Foreperiod and sequential effects: Theory and data. In *Attention and Time* (pp. 289–302). Oxford University Press.

Lucchetti, C., & Bon, L. (2001). Time-modulated neuronal activity in the premotor cortex of macaque monkeys. *Experimental Brain Research*, *141*(2), 254–260. https://doi.org/10.1007/s002210100818

Luce, R. D. (1991). *Response Times: Their Role in Inferring Elementary Mental Organization*. Oxford University Press.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*(1), 24–42. https://doi.org/10.1152/jn.1997.77.1.24

Luck, S. J., Heinze, H. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. *Electroencephalography and Clinical Neurophysiology*, *75*(6), 528–542. https://doi.org/10.1016/0013-4694(90)90139-B

Lundqvist, M., Miller, E. K., Nordmark, J., Liljefors, J., & Herman, P. (2024). Beta: Bursts of cognition. *Trends in Cognitive Sciences*, S1364661324000779. https://doi.org/10.1016/j.tics.2024.03.010

Lundqvist, M., Rose, J., Herman, P., Brincat, S. L., Buschman, T. J., & Miller, E. K. (2016). Gamma and Beta Bursts Underlie Working Memory. *Neuron*, *90*(1), 152–164. https://doi.org/10.1016/j.neuron.2016.02.028

Macar, F., Coull, J., & Vidal, F. (2006). The supplementary motor area in motor and perceptual time processing: fMRI studies. *Cognitive Processing*, *7*(2), 89–94. https://doi.org/10.1007/s10339-005-0025-7

Macar, F., & Vidal, F. (2004). Event-Related Potentials as Indices of Time Processing: A Review. *Journal of Psychophysiology*, *18*(2–3), 89–104. https://doi.org/10.1027/0269-8803.18.23.89

MacKay, A., & Juola, J. F. (2007). Are spatial and temporal attention independent? *Perception & Psychophysics*, *69*(6), 972–979. https://doi.org/10.3758/BF03193935

Manassi, M., Liberman, A., Chaney, W., & Whitney, D. (2017). The perceived stability of scenes: Serial dependence in ensemble representations. *Scientific Reports*, *7*(1), 1971. https://doi.org/10.1038/s41598-017-02201-5
Manassi, M., Murai, Y., & Whitney, D. (2023). Serial dependence in visual perception: A meta-analysis and review. *Journal of Vision*, *23*(8), 18. https://doi.org/10.1167/jov.23.8.18
Manassi, M., & Whitney, D. (2022). Illusion of visual stability through active perceptual serial dependence. *Science Advances*, *8*(2), eabk2480. https://doi.org/10.1126/sciadv.abk2480
Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*(1), 4–18. https://doi.org/10.1111/j.1469-8986.1995.tb03400.x
Mangun, G. R., Hillyard, S. A., & Luck, S. J. (1993). Electrocortical substrates of visual selective attention. In *Attention and performance 14: Synergies in experimental psychology, artificial intelligence, and cognitive neuroscience.* (pp. 219–243). The MIT Press.
Mangun, G. R., Hopfinger, J. B., Kussmaul, C. L., Fletcher, E. M., & Heinze, H.-J. (1997). Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. *Human Brain Mapping*, *5*(4), 273–279. https://doi.org/10.1002/(SICI)1097-0193(1997)5:4<273::AID-HBM12>3.0.CO;2-F
Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024
Martens, S., & Johnson, A. (2005). Timing attention: Cuing target onset interval attenuates the attentional blink. *Memory & Cognition*, *33*(2), 234–240. https://doi.org/10.3758/BF03195312
Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews. Neuroscience*, *5*(3), 229–240. https://doi.org/10.1038/nrn1348
Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology : CB*, *14*(9), 744–751. https://doi.org/10.1016/j.cub.2004.04.028
Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing Type I error and power in linear mixed models. *Journal of Memory and Language*, *94*, 305–315. https://doi.org/10.1016/j.jml.2017.01.001
Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience*, *27*, 307–340. https://doi.org/10.1146/annurev.neuro.27.070203.144247
Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, *29*(6), 317–322. https://doi.org/10.1016/j.tins.2006.04.001
Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Brain Research. Cognitive Brain Research*, *3*(3–4), 227–242. https://doi.org/10.1016/0926-6410(96)00009-2
Mento, G. (2013). The passive CNV: carving out the contribution of task-related processes to expectancy. *Frontiers in Human Neuroscience*, *7*, 827. https://doi.org/10.3389/fnhum.2013.00827
Merchant, H., Harrington, D. L., & Meck, W. H. (2013). Neural Basis of the Perception and Estimation of Time. *Annual Review of Neuroscience*, *36*(1), 313–336. https://doi.org/10.1146/annurev-neuro-062012-170349
Mesulam. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, *10*(4), 309–325. https://doi.org/10.1002/ana.410100402

Mesulam. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*, *28*(5), 597–613. https://doi.org/10.1002/ana.410280502
Mesulam. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *354*(1387), 1325–1346. https://doi.org/10.1098/rstb.1999.0482
Miall, C. (1989). The Storage of Time Intervals Using Oscillating Neurons. *Neural Computation*, *1*(3), 359–371. https://doi.org/10.1162/neco.1989.1.3.359
Michalka, S. W., Kong, L., Rosen, M. L., Shinn-Cunningham, B. G., & Somers, D. C. (2015). Short-Term Memory for Space and Time Flexibly Recruit Complementary Sensory-Biased Frontal Lobe Attention Networks. *Neuron*, *87*(4), 882–892. https://doi.org/10.1016/j.neuron.2015.07.028
Michalka, S. W., Rosen, M. L., Kong, L., Shinn-Cunningham, B. G., & Somers, D. C. (2016). Auditory Spatial Coding Flexibly Recruits Anterior, but Not Posterior, Visuotopic Parietal Cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, *26*(3), 1302–1308. https://doi.org/10.1093/cercor/bhv303
Milliken, B., Lupiáñez, J., Roberts, M., & Stevanovski, B. (2003). Orienting in space and time: Joint contributions to exogenous spatial cuing effects. *Psychonomic Bulletin & Review*, *10*(4), 877–883. https://doi.org/10.3758/BF03196547
Miniussi, C., Wilding, Coull, J., & Nobre, A. (1999). Orienting attention in time Modulation of brain potentials. *Brain*, *122*, 1507–1518.
Miyashita, Y. (1988). Neuronal correlate of visual associative long-term memory in the primate temporal cortex. *Nature*, *335*(6193), 817–820. https://doi.org/10.1038/335817a0
Mok, R. M., Myers, N. E., Wallis, G., & Nobre, A. C. (2016). Behavioral and Neural Markers of Flexible Attention over Working Memory in Aging. *Cerebral Cortex*, *26*(4), 1831–1842. https://doi.org/10.1093/cercor/bhw011
Mondor, T. A., & Amirault, K. J. (1998). Effect of same- and different-modality spatial cues on auditory and visual target identification. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 745–755. https://doi.org/10.1037/0096-1523.24.3.745
Moon, J., & Kwon, O.-S. (2022). Attractive and repulsive effects of sensory history concurrently shape visual perception. *BMC Biology*, *20*(1), 247. https://doi.org/10.1186/s12915-022-01444-7
Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*(1), 152–162. https://doi.org/10.1152/jn.00741.2002
Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science (New York, N.Y.)*, *229*(4715), 782–784. https://doi.org/10.1126/science.4023713
Morey, R. D. (2008). Confidence Intervals from Normalized Data: A correction to Cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, *4*(2), 61–64. https://doi.org/10.20982/tqmp.04.2.p061
Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(42), E8913–E8921. https://doi.org/10.1073/pnas.1705373114
Morillon, B., Hackett, T. A., Kajikawa, Y., & Schroeder, C. E. (2015). Predictive motor control of sensory dynamics in auditory active sensing. *Current Opinion in Neurobiology*, *31*, 230–238. https://doi.org/10.1016/j.conb.2014.12.005

Morillon, B., Schroeder, C. E., Wyart, V., & Arnal, L. H. (2016). Temporal Prediction in lieu of Periodic Stimulation. *The Journal of Neuroscience*, *36*(8), 2342–2347. https://doi.org/10.1523/JNEUROSCI.0836-15.2016
Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., & Husain, M. (2003). The anatomy of visual neglect. *Brain : A Journal of Neurology*, *126*(Pt 9), 1986–1997. https://doi.org/10.1093/brain/awg200
Motala, A., Zhang, H., & Alais, D. (2020). Auditory Rate Perception Displays a Positive Serial Dependence. *I-Perception*, *11*(6), 2041669520982311. https://doi.org/10.1177/2041669520982311
Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, *38*(4), 871–908. https://doi.org/10.1152/jn.1975.38.4.871
Muhle-Karbe, P. S., Myers, N. E., & Stokes, M. G. (2021). A Hierarchy of Functional States in Working Memory. *The Journal of Neuroscience*, *41*(20), 4461–4475. https://doi.org/10.1523/JNEUROSCI.3104-20.2021
Muller, T., & Nobre, A. C. (2014). Perceiving the passage of time: Neural possibilities. *Annals of the New York Academy of Sciences*, *1326*(1), 60–71. https://doi.org/10.1111/nyas.12545
Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M., & Stokes, M. G. (2013). Attention Restores Discrete Items to Visual Short-Term Memory. *Psychological Science*, *24*(4), 550–556. https://doi.org/10.1177/0956797612457782
Musiek, F. E., & Chermak, G. D. (2015). Psychophysical and behavioral peripheral and central auditory tests. *Handbook of Clinical Neurology*, *129*, 313–332. https://doi.org/10.1016/B978-0-444-62630-1.00018-4
Myers, N. E., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2018). Benefits of flexible prioritization in working memory can arise without costs. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(3), 398–411. https://doi.org/10.1037/xhp0000449
Myers, N. E., Rohenkohl, G., Wyart, V., Woolrich, M. W., Nobre, A. C., & Stokes, M. G. (2015). Testing sensory evidence against mnemonic templates. *eLife*, *4*, e09000. https://doi.org/10.7554/eLife.09000
Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, *21*(6), 449–461. https://doi.org/10.1016/j.tics.2017.03.010
Myers, N. E., Stokes, M. G., Walther, L., & Nobre, A. C. (2014). Oscillatory Brain State Predicts Variability in Working Memory. *Journal of Neuroscience*, *34*(23), 7735–7743. https://doi.org/10.1523/JNEUROSCI.4741-13.2014
Nagai, Y., Critchley, H. D., Featherstone, E., Fenwick, P. B. C., Trimble, M. R., & Dolan, R. J. (2004). Brain activity relating to the contingent negative variation: An fMRI investigation. *NeuroImage*, *21*(4), 1232–1241. https://doi.org/10.1016/j.neuroimage.2003.10.036
Nasrawi, R., Boettcher, S. E. P., & Van Ede, F. (2023). Prospection of Potential Actions during Visual Working Memory Starts Early, Is Flexible, and Predicts Behavior. *The Journal of Neuroscience*, *43*(49), 8515–8524. https://doi.org/10.1523/JNEUROSCI.0709-23.2023
Nasrawi, R., & Van Ede, F. (2022). Planning the Potential Future during Multi-item Visual Working Memory. *Journal of Cognitive Neuroscience*, *34*(8), 1534–1546. https://doi.org/10.1162/jocn_a_01875
Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A meta-analysis of executive components of working memory.

Cerebral Cortex (New York, N.Y. : 1991), *23*(2), 264–282. https://doi.org/10.1093/cercor/bhs007
Nee, D. E., & Jonides, J. (2008). Neural correlates of access to short-term memory. *Proceedings of the National Academy of Sciences*, *105*(37), 14228–14233. https://doi.org/10.1073/pnas.0802081105
Nee, D. E., & Jonides, J. (2009). Common and distinct neural correlates of perceptual and memorial selection. *NeuroImage*, *45*(3), 963–975. https://doi.org/10.1016/j.neuroimage.2009.01.005
Nelissen, N., Stokes, M., Nobre, A. C., & Rushworth, M. F. S. (2013). Frontal and Parietal Cortical Interactions with Distributed Visual Representations during Selective Attention and Action Selection. *The Journal of Neuroscience*, *33*(42), 16443–16458. https://doi.org/10.1523/JNEUROSCI.2625-13.2013
Niemi, P., & Naatanen, R. (1981). Foreperiod and Simple Reaction Time. *Psychological Bulletin*, *89*(1), 133–162.
Nobre. (2001). Orienting attention to instants in time. *Neuropsychologia*, *39*(12), 1317–1328. https://doi.org/10.1016/S0028-3932(01)00120-8
Nobre. (2010). How can temporal expectations bias perception and action? In Nobre & Coull (Eds.), *Attention and Time* (1st ed., pp. 371–392). Oxford University PressOxford. https://doi.org/10.1093/acprof:oso/9780199563456.003.0027
Nobre. (2018). Chapter 6: Attention. In *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience* (4th Edition, Vol. 2, pp. 241–316). John Wiley & Sons.
Nobre, A. C., & Stokes, M. G. (2019). Premembering Experience: A Hierarchy of Time-Scales for Proactive Attention. *Neuron*, *104*(1), 132–146. https://doi.org/10.1016/j.neuron.2019.08.030
Nobre, A., Correa, A., & Coull, J. (2007). The hazards of time. *Current Opinion in Neurobiology*, *17*(4), 465–470. https://doi.org/10.1016/j.conb.2007.07.006
Nobre, A., & van Ede, F. (2023). Attention in Flux. *Neuron*.
Nobre, Coull, Maquet, Frith, Vandenberghe, & Mesulam. (2004). Orienting Attention to Locations in Perceptual Versus Mental Representations. *Journal of Cognitive Neuroscience*, *16*(3), 363–373. https://doi.org/10.1162/089892904322926700
Nobre, Gitelman, Dias, & Mesulam. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage*, *11*(3), 210–216. https://doi.org/10.1006/nimg.2000.0539
Nobre, & Kastner. (2014). *The Oxford handbook of attention.* (pp. xvi, 1242). Oxford University Press.
Nobre, & Mesulam. (2014). *Large-scale Networks for Attentional Biases* (Nobre & Kastner, Eds.; Vol. 1). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780199675111.013.035
Nobre, & Rohenkohl. (2014). *Time for the Fourth Dimension in Attention* (Nobre & Kastner, Eds.; Vol. 1). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780199675111.013.036
Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak, & Frith. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain : A Journal of Neurology*, *120 (Pt 3)*, 515–533. https://doi.org/10.1093/brain/120.3.515
Nobre, & van Ede. (2018). Anticipated moments: Temporal structure in attention. *Nature Reviews Neuroscience*, *19*(1), 34–48. https://doi.org/10.1038/nrn.2017.141
Nobre, & van Ede. (2023). Attention in flux. *Neuron*, *111*(7), 971–986. https://doi.org/10.1016/j.neuron.2023.02.032
Noyce, A. L., Cestero, N., Michalka, S. W., Shinn-Cunningham, B. G., & Somers, D. C. (2017). Sensory-Biased and Multiple-Demand Processing in Human Lateral Frontal

Cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *37*(36), 8755–8766. https://doi.org/10.1523/JNEUROSCI.0660-17.2017

Noyce, A. L., Kwasa, J. A. C., & Shinn-Cunningham, B. G. (2023). Defining attention from an auditory perspective. *WIREs Cognitive Science*, *14*(1), e1610. https://doi.org/10.1002/wcs.1610

Oberauer, K. (2019). Working Memory and Attention – A Conceptual Analysis and Review. *Journal of Cognition*, *2*(1), 36. https://doi.org/10.5334/joc.58

Oberauer, K., & Hein, L. (2012). Attention to Information in Working Memory. *Current Directions in Psychological Science*, *21*(3), 164–169. https://doi.org/10.1177/0963721412444727

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*(6753), 584–587. https://doi.org/10.1038/44134

Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, S1364661311000854. https://doi.org/10.1016/j.tics.2011.05.004

Olson, I., & Chun, M. (2001). Temporal Contextual Cuing of Visual Attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *27*(5), 1299–1313. https://doi.org/10.1037//0278-7393.27.5.1299

O'Reilly, J. X., McCarthy, K. J., Capizzi, M., & Nobre, A. C. (2008). Acquisition of the Temporal and Ordinal Structure of Movement Sequences in Incidental Learning. *Journal of Neurophysiology*, *99*(5), 2731–2735. https://doi.org/10.1152/jn.01141.2007

Osada, T., Adachi, Y., Kimura, H. M., & Miyashita, Y. (2008). Towards understanding of the cortical network underlying associative memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1500), 2187–2199. https://doi.org/10.1098/rstb.2008.2271

O'Sullivan, J. A., Power, A. J., Mesgarani, N., Rajaram, S., Foxe, J. J., Shinn-Cunningham, B. G., Slaney, M., Shamma, S. A., & Lalor, E. C. (2015). Attentional Selection in a Cocktail Party Environment Can Be Decoded from Single-Trial EEG. *Cerebral Cortex (New York, N.Y. : 1991)*, *25*(7), 1697–1706. https://doi.org/10.1093/cercor/bht355

Palmieri, H., Fernández, A., & Carrasco, M. (2023). Microsaccades and temporal attention at different locations of the visual field. *Journal of Vision*, *23*(5), 6. https://doi.org/10.1167/jov.23.5.6

Panichello, M. F., & Buschman, T. J. (2021). Shared mechanisms underlie the control of working memory and attention. *Nature*, *592*(7855), 601–605. https://doi.org/10.1038/s41586-021-03390-w

Panichello, M. F., DePasquale, B., Pillow, J. W., & Buschman, T. J. (2019). Error-correcting dynamics in visual working memory. *Nature Communications*, *10*(1), 3366. https://doi.org/10.1038/s41467-019-11298-3

Papadimitriou, C., Ferdoash, A., & Snyder, L. H. (2015). Ghosts in the machine: Memory interference from the previous trial. *Journal of Neurophysiology*, *113*(2), 567–577. https://doi.org/10.1152/jn.00402.2014

Pascucci, D., Mancuso, G., Santandrea, E., Della Libera, C., Plomp, G., & Chelazzi, L. (2019). Laws of concatenated perception: Vision goes for novelty, decisions for perseverance. *PLOS Biology*, *17*(3), e3000144. https://doi.org/10.1371/journal.pbio.3000144

Pascucci, D., Tanrikulu, Ö. D., Ozkirli, A., Houborg, C., Ceylan, G., Zerr, P., Rafiei, M., & Kristjánsson, Á. (2023). Serial dependence in visual perception: A review. *Journal of Vision*, *23*(1), 9. https://doi.org/10.1167/jov.23.1.9

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, *51*(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences*, *13*(4), 160–166. https://doi.org/10.1016/j.tics.2009.01.006

Pessoa, L. (2015). Multiple influences of reward on perception and attention. *Visual Cognition*, *23*(1–2), 272–290. https://doi.org/10.1080/13506285.2014.974729

Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, *45*(14), 1867–1875. https://doi.org/10.1016/j.visres.2005.01.019

Petkov, C. I., Kang, X., Alho, K., Bertrand, O., Yund, E. W., & Woods, D. L. (2004). Attentional modulation of human auditory cortex. *Nature Neuroscience*, *7*(6), 658–663. https://doi.org/10.1038/nn1256

Pfeuffer, C. U., Aufschnaiter, S., Thomaschke, R., & Kiesel, A. (2020). Only time will tell the future: Anticipatory saccades reveal the temporal dynamics of time-based location and task expectancy. *Journal of Experimental Psychology. Human Perception and Performance*, *46*(10), 1183–1200. https://doi.org/10.1037/xhp0000850

Pfeuty, M., Ragot, R., & Pouthas, V. (2005). Relationship between CNV and timing of an upcoming event. *Neuroscience Letters*, *382*(1–2), 106–111. https://doi.org/10.1016/j.neulet.2005.02.067

Pfurtscheller, G., & Berghold, A. (1989). Patterns of cortical activation during planning of voluntary movement. *Electroencephalography and Clinical Neurophysiology*, *72*(3), 250–258. https://doi.org/10.1016/0013-4694(89)90250-2

Pfurtscheller, G., Neuper, C., & Krausz, G. (2000). Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. *Clinical Neurophysiology*, *111*(10), 1873–1879. https://doi.org/10.1016/S1388-2457(00)00428-4

Pfurtscheller, G., Stancák, A. J., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*, *24*(1–2), 39–46. https://doi.org/10.1016/s0167-8760(96)00066-9

Pinchuk-Yacobi, N., Dekel, R., & Sagi, D. (2016). Expectations and visual aftereffects. *Journal of Vision*, *16*(15), 19. https://doi.org/10.1167/16.15.19

Poch, C., Campo, P., & Barnes, G. R. (2014). Modulation of alpha and gamma oscillations related to retrospectively orienting attention within working memory. *European Journal of Neuroscience*, *40*(2), 2399–2405. https://doi.org/10.1111/ejn.12589

Poch, C., Capilla, A., Hinojosa, J. A., & Campo, P. (2017). Selection within working memory based on a color retro-cue modulates alpha oscillations. *Neuropsychologia*, *106*, 133–137. https://doi.org/10.1016/j.neuropsychologia.2017.09.027

Poletti, M., Rucci, M., & Carrasco, M. (2017). Selective attention within the foveola. *Nature Neuroscience*, *20*(10), 1413–1417. https://doi.org/10.1038/nn.4622

Posner, M. I. (1980). Orienting of Attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

Posner, M. I., & Snyder, C. R. R. (2004). *Attention and Cognitive Control.* (p. 223). Psychology Press.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*(1), 23–38. https://doi.org/10.1016/j.neuroscience.2005.06.005

Praamstra, P., Kourtis, D., Kwok, H. F., & Oostenveld, R. (2006). Neurophysiology of implicit timing in serial choice reaction-time performance. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(20), 5448–5455. https://doi.org/10.1523/JNEUROSCI.0440-06.2006

Pratt, C. C. (1930). The spatial character of high and low tones. *Journal of Experimental Psychology*, *13*(3), 278–285. https://doi.org/10.1037/h0072651

Pratt, J., & Abrams, R. A. (1999). Inhibition of return in discrimination tasks. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(1), 229–242. https://doi.org/10.1037/0096-1523.25.1.229

Pylyshyn, Z. (1999). Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *The Behavioral and Brain Sciences*, *22*(3), 341–365; discussion 366-423. https://doi.org/10.1017/s0140525x99002022

Quinn, A. J., van Ede, F., Brookes, M. J., Heideman, S. G., Nowak, M., Seedat, Z. A., Vidaurre, D., Zich, C., Nobre, A. C., & Woolrich, M. W. (2019). Unpacking Transient Event Dynamics in Electrophysiological Power Spectra. *Brain Topography*, *32*(6), 1020–1034. https://doi.org/10.1007/s10548-019-00745-5

Rainer, G., Rao, S. C., & Miller, E. K. (1999). Prospective coding for objects in primate prefrontal cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *19*(13), 5493–5505. https://doi.org/10.1523/JNEUROSCI.19-13-05493.1999

Reddy, L., Kanwisher, N. G., & VanRullen, R. (2009). Attention and biased competition in multi-voxel object representations. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(50), 21447–21452. https://doi.org/10.1073/pnas.0907330106

Rerko, L., & Oberauer, K. (2013). Focused, unfocused, and defocused information in working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *39*(4), 1075–1096. https://doi.org/10.1037/a0031172

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, *27*, 611–647. https://doi.org/10.1146/annurev.neuro.26.041002.131039

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *19*(5), 1736–1753. https://doi.org/10.1523/JNEUROSCI.19-05-01736.1999

Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, *61*(2), 168–185. https://doi.org/10.1016/j.neuron.2009.01.002

Richter, F. R., & Yeung, N. (2014). Neuroimaging studies of task switching. In *Task switching and cognitive control.* (pp. 237–271). Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199921959.003.0010

Riehle, A., Grün, S., Diesmann, M., & Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. *Science (New York, N.Y.)*, *278*(5345), 1950–1953. https://doi.org/10.1126/science.278.5345.1950

Rieke, F., Bodnar, D. A., & Bialek, W. (1997). Naturalistic stimuli increase the rate and efficiency of information transmission by primary auditory afferents. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *262*(1365), 259–265. https://doi.org/10.1098/rspb.1995.0204

Rieth, C. A., & Huber, D. E. (2013). Implicit learning of spatiotemporal contingencies in spatial cueing. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(4), 1165–1180. https://doi.org/10.1037/a0030870

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1A), 31–40. https://doi.org/10.1016/0028-3932(87)90041-8

Rohenkohl, G., Coull, J. T., & Nobre, A. C. (2011). Behavioural Dissociation between Exogenous and Endogenous Temporal Orienting of Attention. *PLoS ONE*, *6*(1), e14620. https://doi.org/10.1371/journal.pone.0014620

Rohenkohl, G., Cravo, A. M., Wyart, V., & Nobre, A. C. (2012). Temporal expectation improves the quality of sensory information. *Journal of Neuroscience*, *32*(24), 8424–8428. https://doi.org/10.1523/JNEUROSCI.0804-12.2012

Rohenkohl, G., Gould, I. C., Pessoa, J., & Nobre, A. C. (2014). Combining spatial and temporal expectations to improve visual perception. *Journal of Vision*, *14*(4), 8–8. https://doi.org/10.1167/14.4.8

Rohenkohl, G., & Nobre, A. C. (2011). Alpha Oscillations Related to Anticipatory Attention Follow Temporal Expectations. *Journal of Neuroscience*, *31*(40), 14076–14084. https://doi.org/10.1523/JNEUROSCI.3387-11.2011

Rolfs, M. (2009). Microsaccades: Small steps on a long way. *Vision Research*, *49*(20), 2415–2441. https://doi.org/10.1016/j.visres.2009.08.010

Rolke, B., Festl, F., & Seibold, V. C. (2016). Toward the influence of temporal attention on the selection of targets in a visual search task: An ERP study: Visual processing enhancements by temporal attention. *Psychophysiology*, *53*(11), 1690–1701. https://doi.org/10.1111/psyp.12734

Rolke, B., & Hofmann, P. (2007). Temporal uncertainty degrades perceptual processing. *Psychonomic Bulletin & Review*, *14*(3), 522–526. https://doi.org/10.3758/BF03194101

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: Correlation or causation? *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(25), 8692–8697. https://doi.org/10.1523/JNEUROSCI.0160-10.2010

Ronnqvist, K. C., McAllister, C. J., Woodhall, G. L., Stanford, I. M., & Hall, S. D. (2013). A Multimodal Perspective on the Composition of Cortical Oscillations. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00132

Rosen, R. (2012). Anticipatory Systems. In R. Rosen (Ed.), *Anticipatory Systems: Philosophical, Mathematical, and Methodological Foundations* (pp. 313–370). Springer New York. https://doi.org/10.1007/978-1-4614-1269-4_6

Rosner, B. (1983). *Percentage Points for a Generalized ESD Many-Outlier Procedure*. *25*(2).

Rösner, M., Sabo, M., Klatt, L.-I., Wascher, E., & Schneider, D. (2022). Preparing for the unknown: How working memory provides a link between perception and anticipated action. *NeuroImage*, *260*, 119466. https://doi.org/10.1016/j.neuroimage.2022.119466

Rucci, M., & Poletti, M. (2015). Control and Functions of Fixational Eye Movements. *Annual Review of Vision Science*, *1*, 499–518. https://doi.org/10.1146/annurev-vision-082114-035742

Ruesseler, M., Weber, L. A., Marshall, T. R., O'Reilly, J., & Hunt, L. T. (2023). Quantifying decision-making in dynamic, continuously evolving environments. *eLife*, *12*, e82823. https://doi.org/10.7554/eLife.82823

Ruff, C. C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J.-D., Rees, G., Josephs, O., Deichmann, R., & Driver, J. (2006). Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Current Biology : CB*, *16*(15), 1479–1488. https://doi.org/10.1016/j.cub.2006.06.057

Rungratsameetaweemana, N., Itthipuripat, S., Salazar, A., & Serences, J. T. (2018). Expectations Do Not Alter Early Sensory Processing during Perceptual Decision-Making. *The Journal of Neuroscience*, *38*(24), 5632. https://doi.org/10.1523/JNEUROSCI.3638-17.2018

Rungratsameetaweemana, N., & Serences, J. T. (2019). Dissociating the impact of attention and expectation on early sensory processing. *Current Opinion in Psychology*, *29*, 181–186. https://doi.org/10.1016/j.copsyc.2019.03.014

Rushworth, Johansen-Berg, H., Göbel, S. M., & Devlin, J. T. (2003). The left parietal and premotor cortices: Motor attention and selection. *NeuroImage*, *20 Suppl 1*, S89-100. https://doi.org/10.1016/j.neuroimage.2003.09.011

Rushworth, Krams, M., & Passingham, R. E. (2001). The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. *Journal of Cognitive Neuroscience*, *13*(5), 698–710. https://doi.org/10.1162/089892901750363244

Saarela, T. P., Niemi, S. M., & Olkkonen, M. (2023). Independent short- and long-term dependencies in perception. *Journal of Vision*, *23*(5), 12. https://doi.org/10.1167/jov.23.5.12

Sahan, M. I., van Dijck, J.-P., & Fias, W. (2022). Eye-movements reveal the serial position of the attended item in verbal working memory. *Psychonomic Bulletin & Review*, *29*(2), 530–540. https://doi.org/10.3758/s13423-021-02005-9

Sailor, K. M., & Antoine, M. (2005). Is memory for stimulus magnitude Bayesian? *Memory & Cognition*, *33*(5), 840–851. https://doi.org/10.3758/BF03193079

Salet, J. M., Kruijne, W., & van Rijn, H. (2021). Implicit learning of temporal behavior in complex dynamic environments. *Psychonomic Bulletin & Review*, *28*(4), 1270–1280. https://doi.org/10.3758/s13423-020-01873-x

Salmelin, R., Hämäläinen, M., Kajola, M., & Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *NeuroImage*, *2*(4), 237–243. https://doi.org/10.1006/nimg.1995.1031

Salmelin, R., & Hari, R. (1994). Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience*, *60*(2), 537–550. https://doi.org/10.1016/0306-4522(94)90263-1

Samaha, J., Bauer, P., Cimaroli, S., & Postle, B. R. (2015). Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction. *Proceedings of the National Academy of Sciences*, *112*(27), 8439–8444. https://doi.org/10.1073/pnas.1503686112

Sanabria, D., Capizzi, M., & Correa, A. (2011). Rhythms that speed you up. *Journal of Experimental Psychology. Human Perception and Performance*, *37*(1), 236–244. https://doi.org/10.1037/a0019956

Saravanan, V., Berman, G. J., & Sober, S. J. (2019). *Application of the Hierarchical Bootstrap to Multi-Level Data in Neuroscience*. https://doi.org/10.1101/819334

Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., Glennon, M., Gerloff, C., Birbaumer, N., & Hummel, F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology : CB*, *19*(21), 1846–1852. https://doi.org/10.1016/j.cub.2009.08.062

Sauter, M., Draschkow, D., & Mack, W. (2020). Building, Hosting and Recruiting: A Brief Introduction to Running Behavioral Experiments Online. *Brain Sciences*, *10*(4), 251. https://doi.org/10.3390/brainsci10040251

Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M., & Turk-Browne, N. B. (2014). The necessity of the medial temporal lobe for statistical learning. *Journal of Cognitive Neuroscience*, *26*(8), 1736–1747. https://doi.org/10.1162/jocn_a_00578

Schapiro, A. C., Kustner, L. V., & Turk-Browne, N. B. (2012). Shaping of Object Representations in the Human Medial Temporal Lobe Based on Temporal Regularities. *Current Biology*, *22*(17), 1622–1627. https://doi.org/10.1016/j.cub.2012.06.056

Schapiro, A. C., Rogers, T. T., Cordova, N. I., Turk-Browne, N. B., & Botvinick, M. M. (2013). Neural representations of events arise from temporal community structure. *Nature Neuroscience*, *16*(4), 486–492. https://doi.org/10.1038/nn.3331

Schapiro, A., & Turk-Browne, N. (2015). Statistical Learning. In *Brain Mapping* (pp. 501–506). Elsevier. https://doi.org/10.1016/B978-0-12-397025-1.00276-1

Schneegans, S., & Bays, P. M. (2017). Neural Architecture for Feature Binding in Visual Working Memory. *The Journal of Neuroscience*, *37*(14), 3913. https://doi.org/10.1523/JNEUROSCI.3493-16.2017

Schneider, D., Barth, A., & Wascher, E. (2017). On the contribution of motor planning to the retroactive cuing benefit in working memory: Evidence by mu and beta oscillatory activity in the EEG. *NeuroImage*, *162*, 73–85. https://doi.org/10.1016/j.neuroimage.2017.08.057

Schneider, D., Mertes, C., & Wascher, E. (2015). On the fate of non-cued mental representations in visuo-spatial working memory: Evidence by a retro-cuing paradigm. *Behavioural Brain Research*, *293*, 114–124. https://doi.org/10.1016/j.bbr.2015.07.034

Schneider, D., Mertes, C., & Wascher, E. (2016). The time course of visuo-spatial working memory updating revealed by a retro-cuing paradigm. *Scientific Reports*, *6*(1), 21442. https://doi.org/10.1038/srep21442

Schoffelen, J.-M., Oostenveld, R., & Fries, P. (2005). Neuronal coherence as a mechanism of effective corticospinal interaction. *Science (New York, N.Y.)*, *308*(5718), 111–113. https://doi.org/10.1126/science.1107027

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition*, *80*(1–2), 1–46. https://doi.org/10.1016/s0010-0277(00)00152-9

Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*, *32*(1), 9–18. https://doi.org/10.1016/j.tins.2008.09.012

Schwartz, O., Hsu, A., & Dayan, P. (2007). *Space and time in visual context.*

Scotti, P. S., Hong, Y., Golomb, J. D., & Leber, A. B. (2021). Statistical learning as a reference point for memory distortions: Swap and shift errors. *Attention, Perception, & Psychophysics*, *83*(4), 1652–1672. https://doi.org/10.3758/s13414-020-02236-3

Seibold, V. C., & Rolke, B. (2014). Does temporal preparation facilitate visual processing in a selective manner? Evidence from attentional capture. *Acta Psychologica*, *151*, 51–61. https://doi.org/10.1016/j.actpsy.2014.05.012

Seibold, V. C., Stepper, M. Y., & Rolke, B. (2020). Temporal attention boosts perceptual effects of spatial attention and feature-based attention. *Brain and Cognition*, *142*, 105570. https://doi.org/10.1016/j.bandc.2020.105570

Serences, J. T. (2008). Value-based modulations in human visual cortex. *Neuron*, *60*(6), 1169–1181. https://doi.org/10.1016/j.neuron.2008.10.051

Serences, J. T., & Boynton, G. M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, *55*(2), 301–312. https://doi.org/10.1016/j.neuron.2007.06.015

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-Specific Delay Activity in Human Primary Visual Cortex. *Psychological Science*, *20*(2), 207–214. https://doi.org/10.1111/j.1467-9280.2009.02276.x

Serences, J. T., Schwarzbach, J., Courtney, S. M., Golay, X., & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, *14*(12), 1346–1357. https://doi.org/10.1093/cercor/bhh095

Seriès, P., & Seitz, A. R. (2013). Learning what to expect (in visual perception). *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00668

Shalev, N., Boettcher, S., Wilkinson, H., Scerif, G., & Nobre, A. C. (2022). Be there on time: Spatial-temporal regularities guide young children's attention in dynamic environments. *Child Development*, *93*(5), 1414–1426. https://doi.org/10.1111/cdev.13770

Shalev, N., Nobre, A. C., & Van Ede, F. (2019). Time for What? Breaking Down Temporal Anticipation. *Trends in Neurosciences*, *42*(6), 373–374. https://doi.org/10.1016/j.tins.2019.03.002

Shdeour, O., Tal-Perry, N., Glickman, M., & Yuval-Greenberg, S. (2024). Exposure to temporal variability promotes subsequent adaptation to new temporal regularities. *Cognition*, *244*, 105695. https://doi.org/10.1016/j.cognition.2023.105695

Sheliga, B. M., Slavutskaya, M. V., Efimova, T. V., Shul'govskii, V. V., & et al. (1994). The effects of visual stimulation pattern on the latency of human saccades. *Sensory Systems*, *8*(1), 35–39.

Shin, J. C., & Ivry, R. B. (2002). Concurrent learning of temporal and spatial sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 445–457. https://doi.org/10.1037/0278-7393.28.3.445

Shin, Law, R., Tsutsui, S., Moore, C. I., & Jones, S. R. (2017). The rate of transient beta frequency events predicts behavior across tasks and species. *eLife*, *6*, e29086. https://doi.org/10.7554/eLife.29086

Shinn-Cunningham, B. G., & Best, V. (2008). Selective Attention in Normal and Impaired Hearing. *Trends in Amplification*, *12*(4), 283–299. https://doi.org/10.1177/1084713808325306

Siegel, M., Donner, T. H., & Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. *Nature Reviews Neuroscience*, *13*(2), 121–134. https://doi.org/10.1038/nrn3137

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are There Multiple Visual Short-Term Memory Stores? *PLOS ONE*, *3*(2), e1699. https://doi.org/10.1371/journal.pone.0001699

Sligte, I. G., Vandenbroucke, A. R., Scholte, H. S., & Lamme, V. (2010). Detailed Sensory Memory, Sloppy Working Memory. *Frontiers in Psychology*, *1*. https://www.frontiersin.org/journals/psychology/articles/10.3389/fpsyg.2010.00175

Sotiropoulos, G., Seitz, A. R., & Seriès, P. (2011). Changing expectations about speed alters perceived motion direction. *Current Biology*, *21*(21), R883–R884. https://doi.org/10.1016/j.cub.2011.09.013

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics*, *78*(7), 1839–1860. https://doi.org/10.3758/s13414-016-1108-5

Spaak, E., de Lange, F. P., & Jensen, O. (2014). Local entrainment of α oscillations by visual stimuli causes cyclic modulation of perception. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *34*(10), 3536–3544. https://doi.org/10.1523/JNEUROSCI.4385-13.2014

Spence, C. J., & Driver, J. (1994). Covert spatial orienting in audition: Exogenous and endogenous mechanisms. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(3), 555–574. https://doi.org/10.1037/0096-1523.20.3.555

Spence, C., & Santangelo, V. (2010). Auditory attention. In C. J. Plack (Ed.), *Oxford Handbook of Auditory Science: Hearing* (p. 0). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780199233557.013.0011

Spencer, R. M. C., & Ivry, R. B. (2009). Sequence learning is preserved in individuals with cerebellar degeneration when the movements are directly cued. *Journal of Cognitive Neuroscience*, *21*(7), 1302–1310. https://doi.org/10.1162/jocn.2009.21102

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research*, *65*(4), 235–241. https://doi.org/10.1007/s004260100059

Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences*, *18*(2), 82–89. https://doi.org/10.1016/j.tics.2013.12.001

Staddon, J. E. R. (2005). Interval timing: Memory, not a clock. *Trends in Cognitive Sciences*, *9*(7), 312–314. https://doi.org/10.1016/j.tics.2005.05.013

Stokes. (2015). 'Activity-silent' working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, *19*(7), 394–405. https://doi.org/10.1016/j.tics.2015.05.004

Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top-down activation of shape-specific population codes in visual cortex during mental imagery. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(5), 1565–1572. https://doi.org/10.1523/JNEUROSCI.4657-08.2009

Stokes, & Nobre. (2012). Top-down biases in visual short-term memory. In *The neuroscience of attention: Attentional control and selection.* (pp. 209–228). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195334364.003.0010

Summerfield, C., & de Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience*, *15*(11), 745–756. https://doi.org/10.1038/nrn3838

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M.-M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, *11*(9), 1004–1006. https://doi.org/10.1038/nn.2163

Sun, J., & Perona, P. (1998). Where is the sun? *Nature Neuroscience*, *1*(3), 183–184. https://doi.org/10.1038/630

Szpiro, S. F. A., Wright, B. A., & Carrasco, M. (2014). Learning one task by interleaving practice with another task. *Vision Research*, *101*, 118–124. https://doi.org/10.1016/j.visres.2014.06.004

Tackett, J. (2024). *ISO 226 Equal-Loudness-Level Contour Signal* [Computer software]. MATLAB Central File Exchange. https://www.mathworks.com/matlabcentral/fileexchange/7028-iso-226-equal-loudness-level-contour-signal

Tal-Perry, N., & Yuval-Greenberg, S. (2022). The Spatiotemporal Link of Temporal Expectations: Contextual Temporal Expectation Is Independent of Spatial Attention. *The Journal of Neuroscience*, *42*(12), 2516–2523. https://doi.org/10.1523/JNEUROSCI.1555-21.2022

Tamber-Rosenau, B. J., Esterman, M., Chiu, Y.-C., & Yantis, S. (2011). Cortical Mechanisms of Cognitive Control for Shifting Attention in Vision and Working Memory. *Journal of Cognitive Neuroscience*, *23*(10), 2905–2919. https://doi.org/10.1162/jocn.2011.21608

Tanji, J. (2001). Sequential Organization of Multiple Movements: Involvement of Cortical Motor Areas. *Annual Review of Neuroscience*, *24*(1), 631–651. https://doi.org/10.1146/annurev.neuro.24.1.631

Taubert, J., Alais, D., & Burr, D. (2016). Different coding strategies for the perception of stable and changeable facial attributes. *Scientific Reports*, *6*(1), 32239. https://doi.org/10.1038/srep32239

Taylor, P. C. J., Nobre, A. C., & Rushworth, M. F. S. (2007). FEF TMS affects visual cortical activity. *Cerebral Cortex (New York, N.Y. : 1991)*, *17*(2), 391–399. https://doi.org/10.1093/cercor/bhj156

Theeuwes, J., Bogaerts, L., & van Moorselaar, D. (2022). What to expect where and when: How statistical learning drives visual selection. *Trends in Cognitive Sciences*, *26*(10), 860–872. https://doi.org/10.1016/j.tics.2022.06.001

Theunissen, F. E., Sen, K., & Doupe, A. J. (2000). Spectral-temporal receptive fields of nonlinear auditory neurons obtained using natural sounds. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *20*(6), 2315–2331. https://doi.org/10.1523/JNEUROSCI.20-06-02315.2000

Thomaschke, R., & Dreisbach, G. (2013). Temporal Predictability Facilitates Action, Not Perception. *Psychological Science*, *24*(7), 1335–1340. https://doi.org/10.1177/0956797612469411

Thomaschke, R., Hoffmann, J., Haering, C., & Kiesel, A. (2016). Time-Based Expectancy for Task Relevant Stimulus Features. *Timing & Time Perception*, *4*(3), 248–270. https://doi.org/10.1163/22134468-00002069

Thomaschke, R., Kiesel, A., & Hoffmann, J. (2011). Response specific temporal expectancy: Evidence from a variable foreperiod paradigm. *Attention, Perception, & Psychophysics*, *73*(7), 2309–2322. https://doi.org/10.3758/s13414-011-0179-6

Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*(1), R11-14. https://doi.org/10.1016/j.cub.2008.10.014

Thut, G., Miniussi, C., & Gross, J. (2012). The functional importance of rhythmic activity in the brain. *Current Biology : CB*, *22*(16), R658-663. https://doi.org/10.1016/j.cub.2012.06.061

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *26*(37), 9494–9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Todorovic, A., & de Lange, F. P. (2012). Repetition suppression and expectation suppression are dissociable in time in early auditory evoked fields. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(39), 13389–13395. https://doi.org/10.1523/JNEUROSCI.2227-12.2012

Todorovic, A., van Ede, F., Maris, E., & de Lange, F. P. (2011). Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: An MEG study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(25), 9118–9123. https://doi.org/10.1523/JNEUROSCI.1425-11.2011

Tong, K., & Dubé, C. (2022). A Tale of Two Literatures: A Fidelity-Based Integration Account of Central Tendency Bias and Serial Dependency. *Computational Brain & Behavior*, *5*(1), 103–123. https://doi.org/10.1007/s42113-021-00123-0

Townsend, J. T., & Ashby, F. G. (1983). *Stochastic modeling of elementary psychological processes*. Cambridge University Press.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the 'internal clock'. *Psychological Monographs: General and Applied*, *77*(13), 1–31. https://doi.org/10.1037/h0093864

Trentin, C., Slagter, H. A., & Olivers, C. N. L. (2023). Visual working memory representations bias attention more when they are the target of an action plan. *Cognition*, *230*, 105274. https://doi.org/10.1016/j.cognition.2022.105274

Treue, S., & Martínez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*(6736), 575–579. https://doi.org/10.1038/21176

Trillenberg, P., Verleger, R., Wascher, E., Wauschkuhn, B., & Wessel, K. (2000). CNV and temporal uncertainty with 'ageing' and 'non-ageing' S1–S2 intervals. *Clinical Neurophysiology*, *111*(7), 1216–1226. https://doi.org/10.1016/S1388-2457(00)00274-1

Triviño, M., Arnedo, M., Lupiáñez, J., Chirivella, J., & Correa, Á. (2011). Rhythms can overcome temporal orienting deficit after right frontal damage. *Neuropsychologia*, *49*(14), 3917–3930. https://doi.org/10.1016/j.neuropsychologia.2011.10.009
Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural Evidence of Statistical Learning: Efficient Detection of Visual Regularities Without Awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945. https://doi.org/10.1162/jocn.2009.21131
Turk-Browne, N. B., Scholl, B. J., Johnson, M. K., & Chun, M. M. (2010). Implicit Perceptual Anticipation Triggered by Statistical Learning. *The Journal of Neuroscience*, *30*(33), 11177. https://doi.org/10.1523/JNEUROSCI.0858-10.2010
van Bergen, R. S., & Jehee, J. F. M. (2019). Probabilistic Representation in Human Visual Cortex Reflects Uncertainty in Serial Decisions. *The Journal of Neuroscience*, *39*(41), 8164–8176. https://doi.org/10.1523/JNEUROSCI.3212-18.2019
van den Brink, R. L., Murphy, P. R., Desender, K., de Ru, N., & Nieuwenhuis, S. (2021). Temporal Expectation Hastens Decision Onset But Does Not Affect Evidence Quality. *The Journal of Neuroscience*, *41*(1), 130. https://doi.org/10.1523/JNEUROSCI.1103-20.2020
van Driel, J., Gunseli, E., Meeter, M., & Olivers, C. N. L. (2017). Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition. *NeuroImage*, *149*, 114–128. https://doi.org/10.1016/j.neuroimage.2017.01.031
van Ede. (2020). Visual working memory and action: Functional links and bi-directional influences. *Visual Cognition*, *28*(5–8), 401–413. https://doi.org/10.1080/13506285.2020.1759744
van Ede, Chekroud, & Nobre. (2019b). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, *3*(5), 462–470. https://doi.org/10.1038/s41562-019-0549-y
van Ede, Chekroud, Stokes, & Nobre. (2019a). Concurrent visual and motor selection during visual working memory guided action. *Nature Neuroscience*, *22*(3), 477–483. https://doi.org/10.1038/s41593-018-0335-6
van Ede, Deden, & Nobre. (2021). Looking ahead in working memory to guide sequential behaviour. *Current Biology*, *31*(12), R779–R780. https://doi.org/10.1016/j.cub.2021.04.063
van Ede, F. (2018). Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: A review. *European Journal of Neuroscience*, *48*(7), 2509–2515. https://doi.org/10.1111/ejn.13759
van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band Oscillations. *The Journal of Neuroscience*, *31*(6), 2016. https://doi.org/10.1523/JNEUROSCI.5630-10.2011
van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal Expectations Guide Dynamic Prioritization in Visual Working Memory through Attenuated α Oscillations. *The Journal of Neuroscience*, *37*(2), 437–445. https://doi.org/10.1523/JNEUROSCI.2272-16.2016
van Ede, F., Quinn, A. J., Woolrich, M. W., & Nobre, A. C. (2018). Neural Oscillations: Sustained Rhythms or Transient Burst-Events? *Trends in Neurosciences*, *41*(7), 415–417. https://doi.org/10.1016/j.tins.2018.04.004
van Ede, F., Rohenkohl, G., Gould, I., & Nobre, A. C. (2020). Purpose-Dependent Consequences of Temporal Expectations Serving Perception and Action. *The Journal of Neuroscience*, *40*(41), Article 41. https://doi.org/10.1523/JNEUROSCI.1134-20.2020

van Ede, & Nobre. (2023). Turning Attention Inside Out: How Working Memory Serves Behavior. *Annual Review of Psychology*, *74*(1), 137–165. https://doi.org/10.1146/annurev-psych-021422-041757

van Elswijk, G., Kleine, B. U., Overeem, S., & Stegeman, D. F. (2007). Expectancy Induces Dynamic Modulation of Corticospinal Excitability. *Journal of Cognitive Neuroscience*, *19*(1), 121–131. https://doi.org/10.1162/jocn.2007.19.1.121

van Loon, A. M., Olmos-Solis, K., & Olivers, C. N. L. (2017). Subtle eye movement metrics reveal task-relevant representations prior to visual search. *Journal of Vision*, *17*(6), 13–13. https://doi.org/10.1167/17.6.13

Van Moorselaar, D., Olivers, C. N. L., Theeuwes, J., Lamme, V. A. F., & Sligte, I. G. (2015). Forgotten but not gone: Retro-cue costs and benefits in a double-cueing paradigm suggest multiple states in visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*(6), 1755–1763. https://doi.org/10.1037/xlm0000124

van Moorselaar, D., & Slagter, H. A. (2019). Learning what is irrelevant or relevant: Expectations facilitate distractor inhibition and target facilitation through distinct neural mechanisms. *The Journal of Neuroscience*, *39*(35), 6953–6967. https://doi.org/10.1523/JNEUROSCI.0593-19.2019

Vangkilde, S., Coull, J. T., & Bundesen, C. (2012). Great expectations: Temporal expectation modulates perceptual processing speed. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(5), 1183–1191. https://doi.org/10.1037/a0026343

Vangkilde, S., Petersen, A., & Bundesen, C. (2013). Temporal expectancy in the context of a theory of visual attention. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1628), 20130054. https://doi.org/10.1098/rstb.2013.0054

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews. Neuroscience*, *2*(4), 229–239. https://doi.org/10.1038/35067550

Vidaurre, D., Hunt, L. T., Quinn, A. J., Hunt, B. A. E., Brookes, M. J., Nobre, A. C., & Woolrich, M. W. (2018). Spontaneous cortical activity transiently organises into frequency specific phase-coupling networks. *Nature Communications*, *9*(1), 2987. https://doi.org/10.1038/s41467-018-05316-z

Wagener, A., & Hoffmann, J. (2010a). Temporal Cueing of Target-Identity and Target-Location. *Experimental Psychology*, *57*(6), 436–445. https://doi.org/10.1027/1618-3169/a000054

Wagener, A., & Hoffmann, J. (2010b). Temporal Cueing of Target-Identity and Target-Location. *Experimental Psychology*, *57*(6), 436–445. https://doi.org/10.1027/1618-3169/a000054

Wallis, G., Stokes, M., Cousijn, H., Woolrich, M., & Nobre, A. C. (2015). Frontoparietal and Cingulo-opercular Networks Play Dissociable Roles in Control of Working Memory. *Journal of Cognitive Neuroscience*, *27*(10), 2019–2034. https://doi.org/10.1162/jocn_a_00838

Wang, M., Huang, Y., Luo, H., & Zhang, H. (2020). Sustained Visual Priming Effects Can Emerge from Attentional Oscillation and Temporal Expectation. *The Journal of Neuroscience*, *40*(18), 3657–3674. https://doi.org/10.1523/JNEUROSCI.2539-19.2020

Ward, L. M., & Lockhead, G. R. (1970). Sequential effects and memory in category judgments. *Journal of Experimental Psychology*, *84*(1), 27–34. https://doi.org/10.1037/h0028949

Ward, L. M., & Lockhead, G. R. (1971). Response system processes in absolute judgment. *Perception & Psychophysics*, *9*(1), 73–78. https://doi.org/10.3758/BF03213031

Warren, S. G., Yacoub, E., & Ghose, G. M. (2014). Featural and temporal attention selectively enhance task-appropriate representations in human primary visual cortex. *Nature Communications*, *5*(1), 5643. https://doi.org/10.1038/ncomms6643

Weber, A. I., Krishnamurthy, K., & Fairhall, A. L. (2019). Coding Principles in Adaptation. *Annual Review of Vision Science*, *5*(1), 427–449. https://doi.org/10.1146/annurev-vision-091718-014818

Webster, M. A. (2015). Visual Adaptation. *Annual Review of Vision Science*, *1*(1), 547–567. https://doi.org/10.1146/annurev-vision-082114-035509

Weinbach, N., Shofty, I., Gabay, S., & Henik, A. (2015). Endogenous temporal and spatial orienting: Evidence for two distinct attentional mechanisms. *Psychonomic Bulletin & Review*, *22*(4), 967–973. https://doi.org/10.3758/s13423-014-0750-y

Wickham, H. (2009). *Ggplot2*. Springer New York, NY. DOI https://doi.org/10.1007/978-0-387-98141-3

Wildegger, T., van Ede, F., Woolrich, M., Gillebert, C. R., & Nobre, A. C. (2017). Preparatory α-band oscillations reflect spatial gating independently of predictions regarding target identity. *Journal of Neurophysiology*, *117*(3), 1385–1394. https://doi.org/10.1152/jn.00856.2016

Wirth, S., Yanike, M., Frank, L. M., Smith, A. C., Brown, E. N., & Suzuki, W. A. (2003). Single neurons in the monkey hippocampus and learning of new associations. *Science (New York, N.Y.)*, *300*(5625), 1578–1581. https://doi.org/10.1126/science.1084324

Wittmann, M. (2013). The inner sense of time: How the brain creates a representation of duration. *Nature Reviews. Neuroscience*, *14*(3), 217–223. https://doi.org/10.1038/nrn3452

Woldorff, M. G., Gallen, C. C., Hampson, S. A., Hillyard, S. A., Pantev, C., Sobel, D., & Bloom, F. E. (1993). Modulation of early sensory processing in human auditory cortex during auditory selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(18), 8722–8726. https://doi.org/10.1073/pnas.90.18.8722

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*(6), 864–871. https://doi.org/10.1038/nn.4546

Womelsdorf, T., Anton-Erxleben, K., Pieper, F., & Treue, S. (2006). Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nature Neuroscience*, *9*(9), 1156–1160. https://doi.org/10.1038/nn1748

Woodrow, H. (1914). The measurement of attention. *The Psychological Monographs*, *17*(5), i–158. https://doi.org/10.1037/h0093087

Woodruff, P. W., Benson, R. R., Bandettini, P. A., Kwong, K. K., Howard, R. J., Talavage, T., Belliveau, J., & Rosen, B. R. (1996). Modulation of auditory and visual cortex by selective attention is modality-dependent. *Neuroreport*, *7*(12), 1909–1913. https://doi.org/10.1097/00001756-199608120-00007

Woods, D. L., Alho, K., & Algazi, A. (1992). Intermodal selective attention. I. Effects on event-related potentials to lateralized auditory and visual stimuli. *Electroencephalography and Clinical Neurophysiology*, *82*(5), 341–355. https://doi.org/10.1016/0013-4694(92)90004-2

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory Biasing of Visuospatial Attention Indexed by Retinotopically Specific α-Bank Electroencephalography Increases over Occipital Cortex. *The Journal of Neuroscience*, *20*(6), RC63–RC63. https://doi.org/10.1523/JNEUROSCI.20-06-j0002.2000

Wöstmann, M., Maess, B., & Obleser, J. (2021). Orienting auditory attention in time: Lateralized alpha power reflects spatio-temporal filtering. *NeuroImage*, *228*, 117711. https://doi.org/10.1016/j.neuroimage.2020.117711

Wurtz, R. H., & Goldberg, M. E. (1972). Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *Journal of Neurophysiology*, *35*(4), 587–596. https://doi.org/10.1152/jn.1972.35.4.587

Wyart, V., Nobre, A. C., & Summerfield, C. (2012). Dissociable prior influences of signal probability and relevance on visual contrast sensitivity. *Proceedings of the National Academy of Sciences*, *109*(9), 3593–3598. https://doi.org/10.1073/pnas.1120118109

Xu, Collins, Khaytin, I., Kaas, J. H., & Casagrande, V. A. (2006). Unequal representation of cardinal vs. Oblique orientations in the middle temporal visual area. *Proceedings of the National Academy of Sciences*, *103*(46), 17490–17495. https://doi.org/10.1073/pnas.0608502103

Xu, Z., Los, S. A., & Theeuwes, J. (2021). Attentional Suppression in Time and Space. *Journal of Experimental Psychology: Human Perception and Performance*, *47*(8), 1056–1062. https://doi.org/10.1037/xhp0000925

Xu, Z., Theeuwes, J., & Los, S. A. (2022). Statistical learning of spatiotemporal regularities dynamically guides visual attention across space. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-022-02573-5

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*(6706), 72–75. https://doi.org/10.1038/23936

Yuval-Greenberg, S., Merriam, E. P., & Heeger, D. J. (2014). Spontaneous Microsaccades Reflect Shifts in Covert Attention. *The Journal of Neuroscience*, *34*(41), 13693. https://doi.org/10.1523/JNEUROSCI.0582-14.2014

Zatorre, R. J., Mondor, T. A., & Evans, A. C. (1999). Auditory attention to space and frequency activates similar cerebral systems. *NeuroImage*, *10*(5), 544–554. https://doi.org/10.1006/nimg.1999.0491

Zhao, J., Al-Aidroos, N., & Turk-Browne, N. B. (2013). Attention Is Spontaneously Biased Toward Regularities. *Psychological Science*, *24*(5), 667–677. https://doi.org/10.1177/0956797612460407

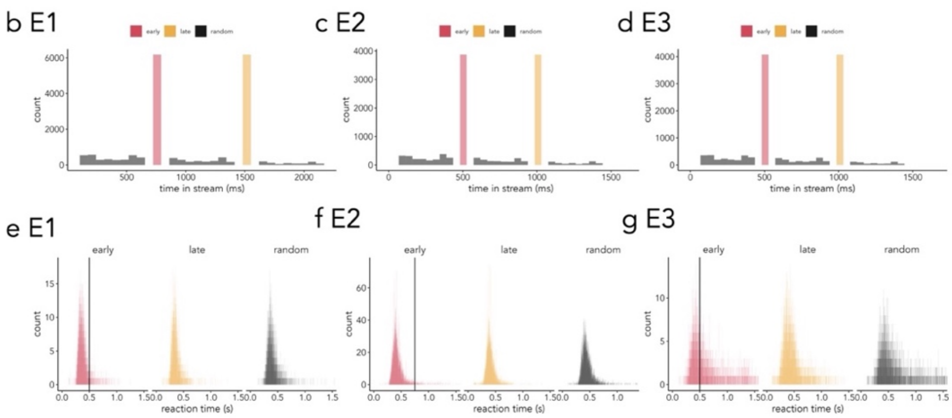
Zokaei, N., Board, A. G., Manohar, S. G., & Nobre, A. C. (2019). Modulation of the pupillary response by the content of visual working memory. *Proceedings of the National Academy of Sciences*, *116*(45), 22802–22810. https://doi.org/10.1073/pnas.1909959116

7 APPENDIX

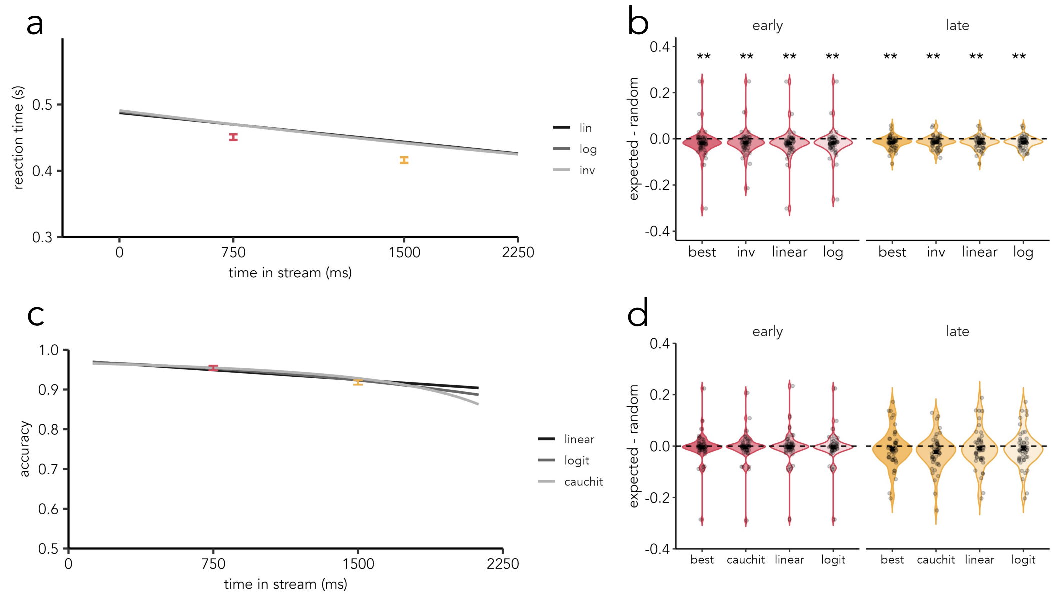
7.1 APPENDIX 1 – CHAPTER 3

a

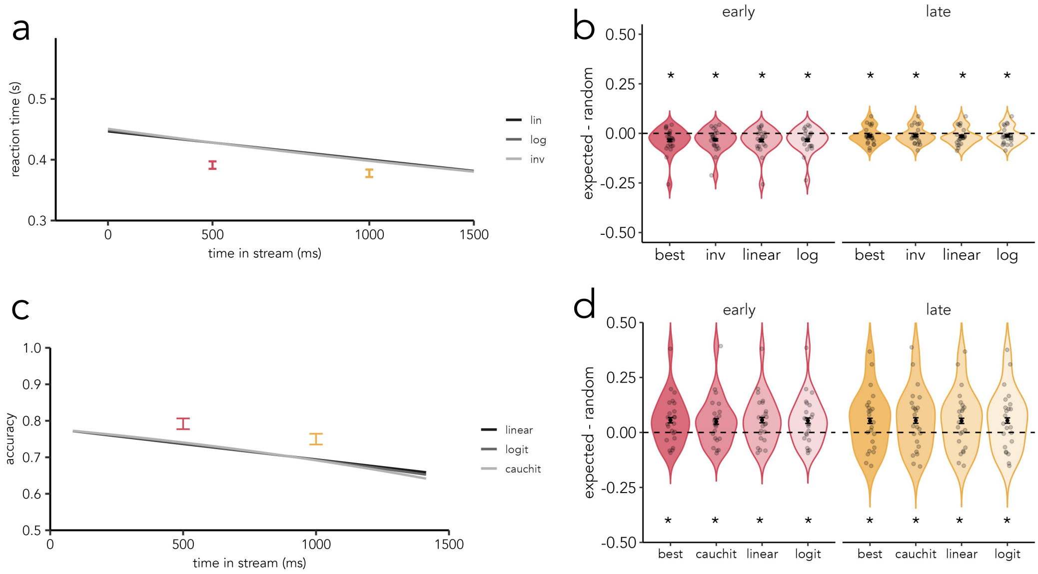
target type	time in stream (ms) E1	time in stream (ms) E2/E3	% cued	% left / right (when cued)	% absent (when cued)
early	*750*	*500*	33.3	43.76 (14.6)	12.5 (4.17)
late	*1500*	*1000*	33.3	43.76 (14.6)	12.5 (4.17)
random	50-700 (50%), 800-1450 (25%), 1550-2000 (12.5%)	50-450 (50%), 550-950 (25%), 1050-1450 (12.5%)	33.3	43.76 (14.6)	12.5 (4.17)



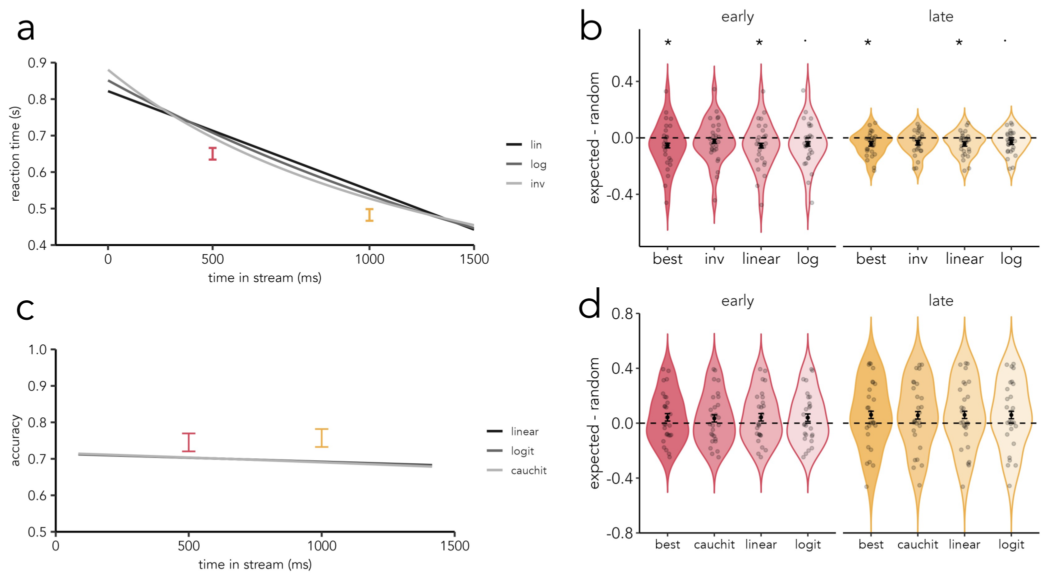
Supplementary Figure 7.1. Chapter 3. Details about trial types and percentages, the timing of targets, and RT distributions. a) Details about trial types and percentages in Experiments 1-3. In each trial, participants were cued and asked to respond to one of three targets which differed in their timing (early, late, and random) and colour (Experiments 1 and 2) or pitch (Experiment 3). One of three targets was cued in each trial and each target type (early, late, and random) was cued in one third of the trials. Thus, each target type was task-relevant only in 33.4% of trials. Each target was absent in 12.5% of all trials and only one target was absent in each trial, thus all three targets were present in 62.5% of trials. Out of the 12.5% of trials in which each target was absent, only a third required a response to the absent target and, therefore, was a no-response trial. Thus, only 12.5% of trials were no-response trials, a third per target type (early, late, and random). Each target type (early, late, and random) appeared on either side equiprobably. b,c,d) Count of trials in which early, late, and random targets appeared at specific times from stream onset (0 s) in Experiments 1, 2 and 3 respectively. e,f,g) Histogram of reaction times (in s) to early, late, and random targets across participants in Experiments 1, 2 and 3, respectively. The vertical line on the first panel reflects the time of late target appearance.



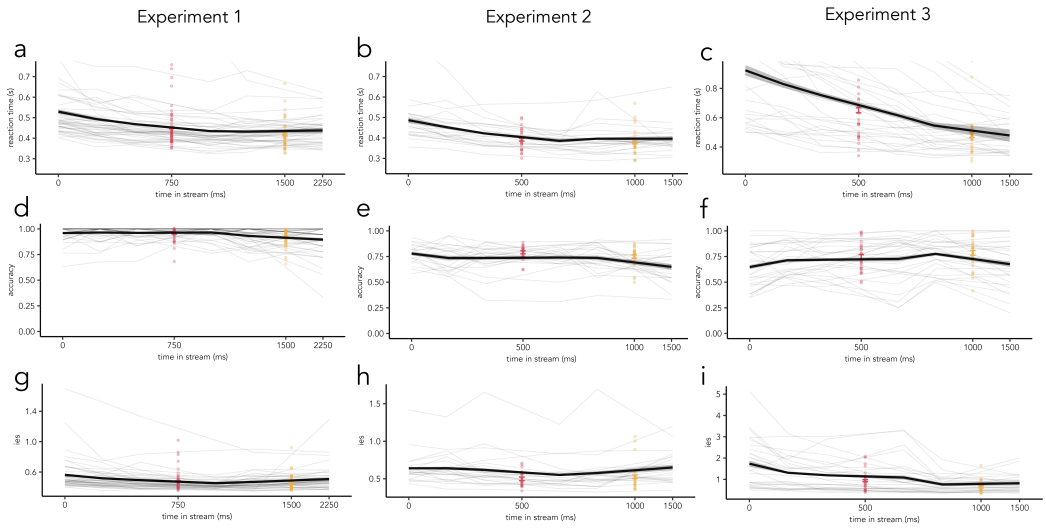
Supplementary Figure 7.2. Chapter 3. Online visual task accuracy, and RT results using GLMs with different link functions. a) GLM fits of RT to random targets as a function of target onset and mean RT to early (pink) and late (yellow) targets across participant (error bars represent SEM). Differently coloured lines represent the GLM fits with the different link functions: linear, logarithmic, and inverse**.** b) Difference between RT at the time of early/late targets as estimated from participant-specific GLMs (linear, logarithmic, inverse, and participant-specific best fit) and actual RT to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: main effect of time ($F(1,48) = 27.77$, $***p < .001$, $\eta^2 = .04$), main effect of predictability ($F(1,48) = 8.14$, $**p = .006$, $\eta^2 = .01$) and no interaction between the factors ($F(1,48) = .1$, $p = .7$, $\eta^2 < .000$). Inverse fit: main effect of time ($F(1,48) = 31$, $***p < .001$, $\eta^2 = .044$), main effect of predictability ($F(1,48) = 7.92$, $**p = .007$, $\eta^2 = .008$) and no interaction between the factors ($F(1,48) = .05$, $p = .8$, $\eta^2 < .000$). Logarithmic fit: main effect of time ($F(1,48) = 27.66$, $***p < .001$, $\eta^2 = .044$), main effect of predictability ($F(1,48) = 8.84$, $**p = .005$, $\eta^2 = .01$) and no interaction between the factors ($F(1,48) = .1$, $p = .7$, $\eta^2 < .000$). c) GLM fits of accuracy to random targets as a function of target onset and mean accuracy to early (pink) and late (yellow) targets across participants (error bars represent SEM). Differently coloured thick lines represent GLM fits with the different link functions: linear, logit, and cauchit. d) Difference between accuracy at the time of early/late targets as estimated from participant specific GLMs (linear, logit, cauchit, and participant-specific best fit) and actual accuracy to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: main effect of time ($F(1,48) = 15.1$, $***p < .001$, $\eta^2 = .06$), no main effect of predictability ($F(1,48) = .8$, $p = .38$, $\eta^2 = .003$) and no interaction between the factors ($F(1,48) = .027$, $p = .6$, $\eta^2 < .000$). Cauchit fit: main effect of time ($F(1,48) = 14.27$, $***p < .001$, $\eta^2 = .045$), no main effect of predictability ($F(1,48) = 3.16$, $p = .08$, $\eta^2 = .01$) and an interaction between both factors ($F(1,48) = 4.34$, $*p = .04$, $\eta^2 = .005$). Logit fit: main effect of time (F(1,48) = 15.1, ***p < .001, η^2 = .06), no main effect of predictability (F(1,48) = .78, p = .37, η^2 = .003) and no interaction between the factors (F(1,48) = .027, p = .6, η^2 < .000).



Supplementary Figure 7.3. Chapter 3. In-person visual task accuracy, and RT results using GLMs with different link functions. a) GLM fits of RT to random targets as a function of target onset and mean RT to early (pink) and late (yellow) targets across participants (error bars represent SEM). Differently coloured lines represent GLM fits with the different link functions: linear, logarithmic, and inverse. b) Difference between RT at the time of early/late targets as estimated from participant specific GLMs (linear, logarithmic, inverse, and participant-specific best fit) and actual RT to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: main effect of time (F(1,22) = 9.7, **p = .005, η^2 = .037), main effect of predictability (F(1,22) = 5.83, *p = .02, η^2 = .034) and no interaction between the factors (F(1,22) = 4.19, p = .05, η^2 = .008). Inverse fit: main effect of time (F(1,22) = 9.8, **p = .004, η^2 = .038), main effect of predictability (F(1,22) = 5.7, *p = .02, η^2 = .03) and an interaction between the factors (F(1,22) = 4.5, *p = .045, η^2 = .008). Logarithmic fit: main effect of time (F(1,22) = 9.66, **p = .005, η^2 = .038), main effect of predictability (F(1,22) = 6.11, *p = .02, η^2 = .033) and no interaction between the factors (F(1,22) = 4.28, p = .05, η^2 = .008). c) GLM fits of accuracy to random targets as a function of target onset and mean accuracy to early (pink) and late (yellow) targets across participants (error bars represent SEM). Differently coloured lines represent GLM fits with the different link functions: linear, logit, and cauchit. d) Difference between accuracy at the time of early/late targets as estimated from participant specific GLMs (linear, logit, cauchit, and participant-specific best fit) and actual accuracy to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: main effect of time (F(1,22) = 5.67, *p = .02, η^2 = .043), main effect of predictability (F(1,22) = 5.52, *p = .03, η^2 = .07) and no interaction between the factors (F(1,22) = .02, p = .89, η^2 < .000).=. Cauchit fit: main effect of time (F(1,22) = 6.55, *p = .02, η^2 = .05), main effect of predictability (F(1,22) = 4.88, *p = .04, η^2 = .067) and no interaction between the factors (F(1,22) = .035, p = .85, η^2 < .000). Logit fit: main effect of time (F(1,22) = 6.1, *p = .02, η^2 = .046), main effect of predictability (F(1,22) = 5.35, *p = .03, η^2 = .074) and no interaction between the factors (F(1,22) = .0003, p = .98, η^2 < .000).

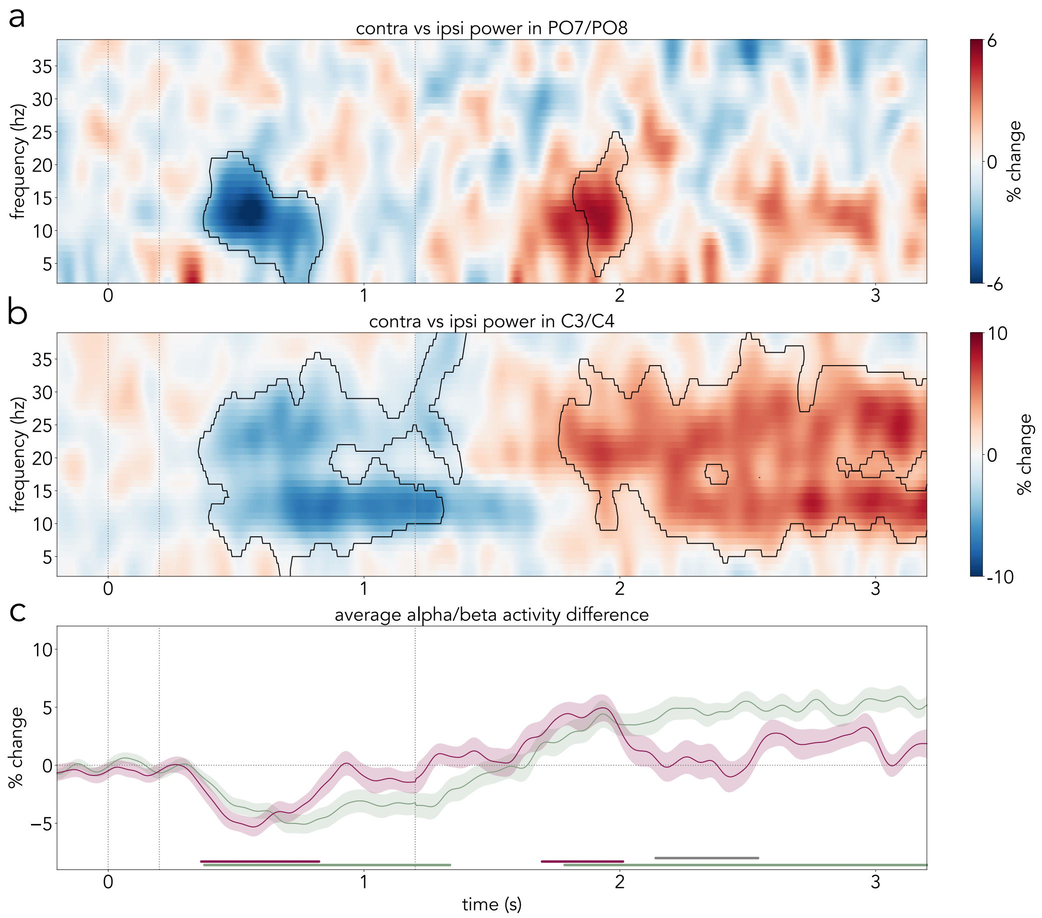


Supplementary Figure 7.4. Chapter 3. In-person auditory task accuracy and RT results using GLMs with different link functions. a) GLM fits of RT to random targets as a function of target onset and mean RT to early (pink) and late (yellow) targets across participants (error bars represent SEM). Differently coloured lines represent GLM fits with the different link functions: linear, logarithmic, and inverse. b) Difference between RT at the time of early/late targets as estimated from participant specific GLMs (linear, logarithmic, inverse, and participant-specific best fit) and actual RT to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: main effect of time (F(1,26) = 53.12, ***p < .001, η^2 = .15), main effect of predictability (F(1,26) = 5.67, *p = .02, η^2 = .014) and no interaction between both factors (F(1,26) = .14, p = .7, η^2 < .000). Inverse fit: main effect of time (F(1,26) = 58.6, ***p < .001, η^2 = .15), no main effect of predictability (F(1,26) = 2.18, p = .15, η^2 = .005) and no interaction between the factors (F(1,26) = .17, p = .7, η^2 = .0002). Logarithmic fit: main effect of time (F(1,26) = 54.6, ***p < .001, η^2 = .16), a trend towards a main effect of predictability (F(1,26) = 6.11, p = .08, η^2 = .009) and no interaction between the factors (F(1,26) = .16, p = .7, η^2 = .0002). c) GLM fits of accuracy to random targets as a function of target onset and mean accuracy to early (pink) and late (yellow) targets across participants (error bars represent SEM). Differently coloured lines represent GLM fits with the different link functions: linear, logit, and cauchit. d) Difference between accuracy at the time of early/late targets as estimated from participant specific GLMs (linear, logit, cauchit, and participant-specific best fit) and actual accuracy to early/late targets. Results from 2x2 ANOVAs with time and predictability as factors for the different fits. Best fit: no main effect of time (F(1,26) = .02, p = .9, $\eta^2 < .000$), no main effect of predictability (F(1,26) = 2.38, p = .14, $\eta^2 = .002$) and no interaction between the factors (F(1,26) = .13, p = .72, $\eta^2 < .000$). Cauchit fit: no main effect of time (F(1,26) = .0007, p = .98, $\eta^2 < .000$), no main effect of predictability (F(1,26) = 1.81, p = .18, $\eta^2 = .002$) and no interaction between the factors (F(1,26) = .2, p = .65, $\eta^2 = .001$). Logit fit: no main effect of time (F(1,26) = .01, p = .91, $\eta^2 < .000$), no main effect of predictability (F(1,26) = 2.2, p = .15, $\eta^2 = .002$) and no interaction between the factors (F(1,26) = .15, p = .7, $\eta^2 < .000$).

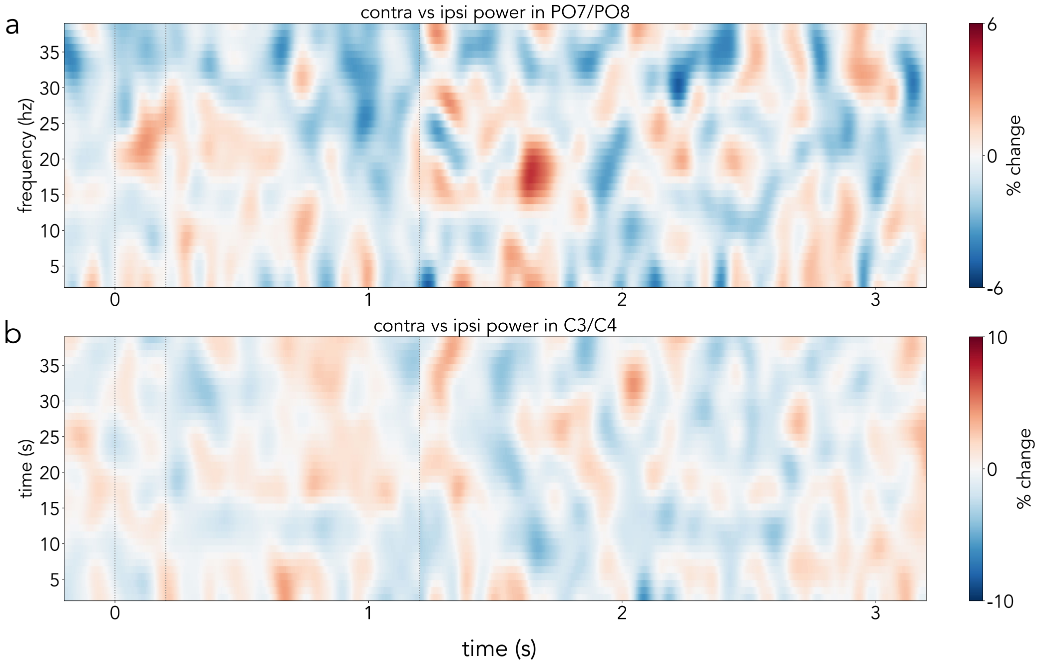


Supplementary Figure 7.5. Chapter 3. Reaction time (s), accuracy and inverse efficiency score (IES) as a function of binned time-in-stream in Experiments 1 (left column), 2 (central column) and 3 (right column). Time-in-stream was split into 8 bins corresponding to targets that occurred in the following bins: *Experiment 1*: 0-0.24 s, 0.24-0.44 s, 0.44-0.7 s, 0.7-0.8 s (early), 0.8-1.1 s, 1.1-1.45 s, 1.45-1.55 s (late) and 1.55-2.25. *Experiments 2 and 3*: 0-0.15 s, 0.15-0.3 s, 0.3-0.45 s, 0.45-0.55 s (early), 0.55-0.75 s, 0.75-0.95 s, 0.95-1.05 s (late) and 1.05-1.5 s. RT (a, b, c), accuracy (d, e, f), and a IES (g, h, i; Townsend & Ashby, 1983) was calculated in each bin and plotted for each participant in the random (grey lines), early (pink dots) and late (yellow dots) conditions. The participant average for the random (thick black line), early (pink) and late (yellow) conditions is shown with error bars and shaded areas representing the SEM.

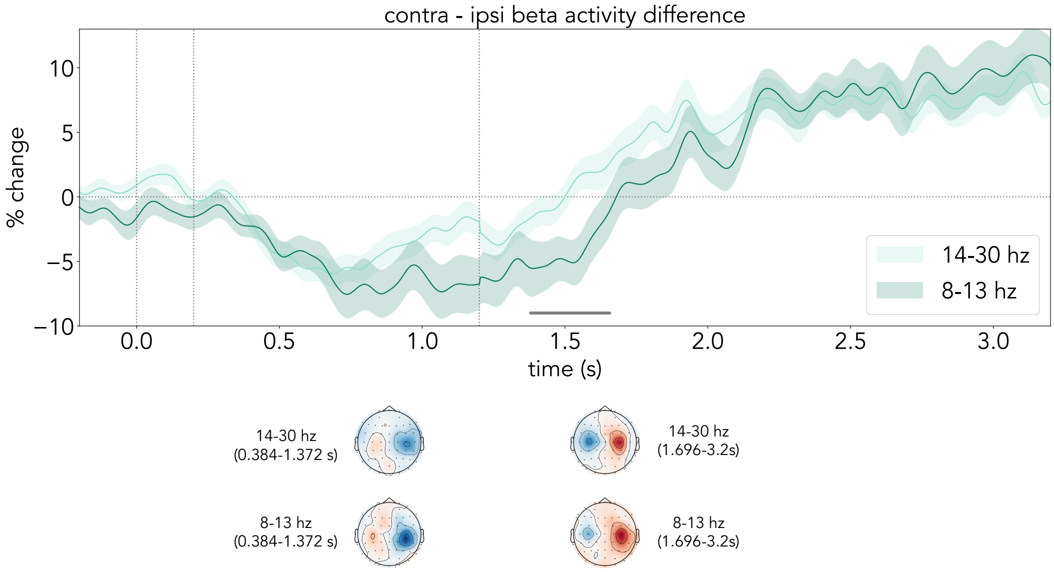
7.2 APPENDIX 2 – CHAPTER 4



Supplementary Figure 7.6. Chapter 4 (Experiment 1). Frequency-specific EEG activity locked to cue onset in informative trials in a cluster of visual/motor EEG electrodes. a) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued bar location in two clusters of lateralised occipital sensors (L: O1, PO7, PO3; R: O2, PO8, PO4) divided by summed contralateral and ipsilateral activity and expressed as a percentage. Black outline indicates statistically significant clusters. b) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued prospective action in two clusters of lateralised central sensors (L: C1, C3, CP1, CP3; R: C2, C4, CP2, CP4) divided by summed contralateral and ipsilateral activity and expressed as a percentage. Black outline indicates statistically significant clusters. c) Average alpha (8-12 hz) activity difference between contralateral and ipsilateral sensors to the cued location across participants (burgundy) and average mu-beta (8-30 hz) activity between contralateral and ipsilateral sensors to the cued action across participants (green). Shaded areas represent the SEM and cluster-based permutation-corrected significant time points are indicated with horizontal lines (burgundy: alpha vs null; green: mu-beta vs null; grey: alpha vs mu-beta). The first part of the time-frequency spectra in panels a and b and of the time course in c (-0.2-1.2 s) corresponds to the average of short and long trials, and the second part (1.2-3.2 s) corresponds to long trials only. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the retro-cue and the time of probe appearance in early trials (1.2 s).



Supplementary Figure 7.7. Chapter 4 (Experiment 1). Frequency-specific EEG activity locked to cue onset in noninformative trials, where no location/action is systematically prioritised. a) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued bar location in occipital sensors (PO7, PO8) divided by summed contralateral and ipsilateral activity and expressed as a percentage. b) Contrast between EEG time-frequency activity contralateral vs ipsilateral to the cued prospective action in central sensors (C3, C4) divided by summed contralateral and ipsilateral activity and expressed as a percentage. The first part of the time-frequency spectra (-0.2-1.2 s) corresponds to the average of short and long trials, and the second part (1.2-3.2 s) corresponds to long trials only. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the noninformative cue and the time of probe appearance in early trials (1.2 s). No significant clusters were found.



Supplementary Figure 7.8. Chapter 4 (Experiment 1). Average mu (8-12 Hz) and beta (13-30 Hz) EEG activity locked to cue onset in informative trials. Average mu (8-12 Hz; dark green) and beta (13-30 Hz; light green) activity difference between contralateral and ipsilateral sensors to the cued action across participants. Shaded areas represent the SEM and cluster-based permutation-corrected significant time points are indicated with horizontal lines (mu vs beta). The first part of the time course (-0.2-1.2 s) corresponds to the average of short and long trials, and the second part (1.2-3.2 s) corresponds to long trials only. The vertical dotted lines represent (from left to right) the onset (0 s) and offset (0.2 s) of the retro-cue and the time of probe appearance in early trials (1.2 s). Topographies represent the average mu (bottom) and beta (top) activity in left-versus-right contrasts across all sensors during the specified time-windows which correspond to the mu-beta clusters in Figure 4.2.