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Tracking the Mind's Eye

Eye movements during mental imagery and
memory retrieval



LUND
UNIVERSITY

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Humaniora och Teologi, Filosofiska institutionen
Avdelningen för kognitionsvetenskap
Lund University 2013

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I had expected something, but not Nothing.

I had expected almost anything, but not Nothing.

Prepared for attendance and appreciation, my mind could not undo its readiness for perception and accept the unfulfilled preparation for painting it encountered.

Here was a qualified Nothing, a Nothing of such deep despair, I could not be absolved of my aesthetic responsibility – a nonhope Nothing, a non-Nothing – and yet, also before my eyes was the evidence of a dedication to artistic expression so unyieldingly vast in its implications that my mind – at least first – bluntly refused to accept the evidence.

from *The Burnt Orange Heresy*
by Charles Willeford

Abstract

This thesis investigates the relationship between eye movements, mental imagery and memory retrieval in four studies based on eye-tracking experiments.

The first study is an investigation of eye movements during mental imagery elicited both visually and verbally. The use of complex stimuli and the development of a novel method where eye movements are recorded concurrently with verbal data enabled the above-mentioned relationship to be studied to an extent going beyond what previous research had been able to do. Eye movements were found to closely reflect content and spatial layout while participants were listening to a spoken scene description, while they were describing the same scene from memory, and while they were describing a picture they had previously seen. This effect was equally strong during recall from memory irrespective of whether the scene visualised had originally been inspected visually by the participants or whether it was constructed whole-cloth from long-term memory (on the basis of a spoken scene description that the participants had previously listened to). It was also found that eye movements "to nothing" appeared both when the participants were visualising scenes while looking at a blank screen and when they were doing so in complete darkness.

The second study explored an effect frequently observed in the first study, involving a "scaling-down" during recall of participants' gaze patterns to an area smaller than that occupied by the stimulus encoded. It was found that this scaling effect correlated with spatial-imagery ability: the gaze patterns of participants with weaker spatial-imagery ability were closer in size to the encoded scene than the gaze patterns of those stronger in spatial-imagery ability.

In the third study, the role of eye movements during mental imagery was investigated in four experiments where eye movements were prohibited during either the encoding phase or the recall phase. Experiments 1 and 2 showed that maintaining central fixation during visual or auditory encoding, respectively, had no effect on how eye movements were executed during recall. Thus, oculomotor events during recall are not reproductions of those produced during encoding. In Experiments 3 and 4, central fixation was instead maintained during recall. This turned out to alter and impair scene recollection, irrespective of the modality of encoding.

Finally, in the fourth study, the functional role of eye movements in relation to memory retrieval was further investigated by means of direct eye-movement manipulation in the retrieval phase of an episodic-memory task. Four conditions were used: (1) free viewing on a blank screen, (2) maintaining central fixation, (3) viewing within a square congruent with the location of the objects to be recalled, and (4) viewing within a square incongruent with the location of the objects to be recalled. The results obtained show that gaze position plays an active and facilitatory role during memory retrieval.

The findings from these studies are discussed in the light of current theories regarding eye movements during mental imagery and memory retrieval.

KEY WORDS: Mental Imagery, Eye Movements, Eye-tracking, Encoding, Recall, Memory Retrieval, Episodic Memory

Sammanfattning

Denna avhandling behandlar fyra olika studier som med hjälp av ögonrörelsemätning (eye-tracking) undersöker sambandet mellan blickbeteende, mentala bilder och minne.

I den första studien undersöktes blickbeteendet för ett antal forskningspersoner samtidigt som de målade upp mentala bilder i sin "inre värld". Detta gjordes med hjälp av en metod som kombinerar verbal data med ögonrörelsemätningar. Resultaten visar att forskningspersonernas ögonrörelser spontant återspeglade både innehåll och rumsliga relationer ifrån deras visualiseringar. Denna företeelse var påtaglig och lika stark i tre olika situationer: när de lyssnade på en scenbeskrivning, när de själva återberättade samma scenbeskrivning och när de muntligt beskrev en bild som de tidigare sett. Det visade sig att detta fenomen av ögonrörelser till "ingenting" skedde oavsett om de tittade på en blank skärm eller om de befann sig i ett rum som var totalt mörklagt.

Den andra studien utforskade en specifik företeelse som observerades i den första studien, nämligen att flera av forskningspersonerna "skalade ner" sina ögonrörelser och tittade på en yta som var påtagligt mindre än den återkallade bildens originalstorlek. Resultat från studie två visar att denna nedskalning korrelerade med forskningspersonernas rumsliga visualiseringsförmåga: De med svag rumslig visualiseringsförmåga tittade på en yta som låg närmare bildens originalstorlek än de med stark rumslig visualiseringsförmåga.

I den tredje studien undersöktes själva betydelsen av att göra ögonrörelser under sådana mentala visualiseringar som utforskades i studie ett och två. Metoden för att genomföra detta var att låta begränsa forskningspersonernas tittande, antingen när de "kodade in" en scen eller när de återkallade den. Resultat från studie tre visar att spontana ögonrörelser som reflekterade minnesåterkallningen uppstod trots att de hindrades att flytta blicken under inkodningen. Alltså är ögonrörelser under mentala visualiseringar inte endast en återuppspelning av de ögonrörelser som produceras när vi kodar in en scen. När forskningspersonerna istället hindrades från att flytta blicken under minnesåterkallningen visade det sig att detta förändrade och försämrade deras förmåga att visualisera scenen. Detta antyder att ögonrörelser har en funktionell roll när vi spelar upp mentala visualiseringar i vår "inre värld".

I den fjärde och sista studien utforskades relationen mellan blickbeteende och minnesåterkallning mer utförligt med hjälp av en ny experimentdesign och med olika typer av ögonrörelsemanipulationer. Först inspekterade forskningspersonerna ett antal objekt på en datorskärm. Dessa objekt återkallades sedan under följande förhållanden: (1) fritt tittande på en tom skärm, (2) fixerande av en punkt i mitten av skärmen, (3) tittande på en tom yta som sammanföll med positionen som det återkallade objektet befann sig på under inspektionsfasen, och (4) tittande på en tom yta som inte sammanföll med positionen som det återkallade objektet befann sig på under inspektionsfasen. Resultat från studie fyra visar att beroende på var och hur man tittar så kan man förbättra eller försämma minnesprestationen. Detta styrker slutsatsen från studie tre om att blickbeteende har en funktionell roll när vi minns och visualiserar händelser.

I avhandlingen diskuteras de fyra studiernas resultat utifrån aktuella teorier om mentala bilder och minnesåterkallning.

Acknowledgments

Many of my colleagues, friends and family members have contributed in various ways along the journey that eventually became this thesis. I am extremely grateful for all your help, feedback, criticism and support. However, some of the contributions deserve a few extra words of acknowledgement.

First and foremost, I would like to thank my supervisors, Jana Holšánová and Kenneth Holmqvist. You have both been there by my side from day one and you have always taken your time to discuss my work with me and to give me feedback on it. Your support, your critical minds and your advice have meant so much to me, and this thesis would not have been possible without you. I am infinitely thankful to both of you. Tack för allt!

Second, over the years I have also worked in a different research project where we study the process of writing. This project has been headed by Åsa Wengelin, who has been my third supervisor in many ways (though not officially). Åsa, you have helped me on so many levels during these years and I have learned so much from you. You have been a great role model for how to find one's way in the world of academia and how to be a good researcher. I cannot thank you enough. Stort stort tack för allt!

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The study presented in the last paper (Paper IV) included in this thesis was conducted in collaboration with Mikael Johansson. Mikael, thanks for all the stimulating discussions we have had over the past two years. It has been a true pleasure working with you. Stort tack!

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The work presented in this thesis has largely been conducted within the multidisciplinary and cross-faculty research environment called Thinking in Time: Cognition, Communication and Learning (CCL). It has been very useful and inspiring to work in an environment like this, where we exchange ideas, theories and methods from disciplines as diverse as psychology, linguistics, neurophysiology, logopedics, audiology and cognitive science. Thank you, all CCL members! It has been a great ride!

Over the years I have had the privileged opportunity to travel and present my work at many international conferences, workshops and meetings. Many people have contributed their knowledge and comments, substantially improving the work presented in this thesis. However, I am especially grateful to Agnes Scholz. We have presented our respective research during the same session on many occasions, and the discussions we have had have always been very enjoyable and helpful. Vielen Dank Agnes!

If you enjoy reading this thesis, I suspect this is largely due to Johan Segerbäck, who has checked my English and proof-read it. Johan, you do such great work and I am very thankful for how much you have improved the text. Stort tack! Also, a big thank-you to the ever-helpful Johan Cedervall at E-huset, who handled the actual printing of this thesis. Tack!

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List of original papers

This thesis is based on the papers listed below, which will be referred to as "Paper I", etc., throughout the thesis.

- Paper I.** Johansson, R., Holsanova, J., & Holmqvist, K. (2006). Pictures and Spoken Descriptions Elicit Similar Eye Movements During Mental Imagery, Both in Light and in Complete Darkness. *Cognitive Science*, 30(6), 1053–1079. doi: 10.1207/s15516709cog0000_86
- Paper II.** Johansson, R., Holsanova, J., & Holmqvist, K. (2011). The dispersion of eye movements during visual imagery is related to individual differences in spatial imagery ability. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd Annual Meeting of the Cognitive Science Society* (pp. 1200–1205). Austin, TX: Cognitive Science Society.
- Paper III.** Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *Journal of Experimental Psychology: Human Perception & Performance*. 38(5), 1289–1314. doi: 10.1037/a0026585
- Paper IV.** Johansson, R., & Johansson, M. (2013). Look here, eye movements play a functional role in memory retrieval. *Psychological Science*. doi: 10.1177/0956797613498260

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Chapter 1

Introduction

Please answer the following questions: What are the colours of Spider-Man's costume? Does Zlatan Ibrahimović wear glasses? Which are darker, coffee beans or hazelnuts? Is Stockholm further north or south than London? To perform that task you probably visualised, or saw with your "mind's eye", Spider-Man, Zlatan Ibrahimović, coffee beans and hazelnuts, and a map of Europe. Although the "visual" impressions we derive from such acts of visualisation may seem less detailed and appear to fade faster than when we look at things in the "real" world, we still experience them as quite realistic. The ability to form mental images of objects, people and scenes from memory in this way is a cognitive tool which we use in a wide range of activities – for example, when recollecting childhood memories, when deciding whether a painting would look good in our home, when solving mechanical problems, and even when putting ourselves in other people's shoes.

Now, instead of visualising something yourself, tell a friend to imagine her home and then ask her how many windows there are. Then tell her to imagine a map of the world and ask her to indicate the relative locations of Sweden, Italy, Libya and South Africa. If you look at her eyes while she is performing those tasks, you will probably see them moving as she is mentally "counting" windows and "scanning" a world map. Moreover, if you had been able to record her eye movements during this procedure, you would most likely have found that the directions of those movements and the points where she rested her gaze showed a pattern corresponding to the spatial layout of her visualisations. For instance, the window counting is likely to elicit horizontal eye movements while the map scanning is likely to elicit more vertical eye movements.

This phenomenon – that eye movements can be used as a direct behavioural correlate of humans' internal shifts of attention when they look "at nothing" while visualising objects and scenes from memory – is what I will investigate and discuss in this thesis.

1.1 Scope of the thesis

To investigate the relationship between mental imagery, memory retrieval and eye movements, I will refer to a series of empirical studies originally presented in four different papers reporting a total of ten experiments carried out in the Humanities Laboratory at Lund University, Sweden.

When interpreting the results of those experiments, I will not argue in favour of any specific model or theory of cognition. Instead, my main aim will be to identify general principles that apply to eye movements during mental imagery and memory retrieval. I will then evaluate how well those principles fit with various current theories. I believe that such a perspective, where the characterisation of general principles is favoured over specific models, is the most appropriate approach in experimental research. This is because any other approach entails a risk that the researcher's favourite theories will exert undue influence on his or her research, which may in turn cause interpretations of results to become biased. Indeed, experiments are sometimes even designed beforehand to fit specific theories, in which case the model for which researchers are trying to find support may actually prevent them from noticing interesting results.

In research on mental imagery, Ronald A. Finke and Martha J. Farah are two established and well-known researchers whose approach to empirical research has greatly influenced and inspired me. They have both carried out high-quality empirical work, and even though both of them have supported a specific camp in the "mental imagery debate" (see Section 2.1.4 below), the foundation of their research has been the systematic investigation of how general principles of mental imagery work and how they relate to the human brain. My ambition, in the studies included in this thesis, has been to carry out research in the same tradition. I will thus try to let the findings "speak for themselves", instead of claiming that they constitute proof of a certain model or theory.

I consider myself a cognitive scientist who mostly uses tools from behavioural research and cognitive psychology. Specifically, I use eye-tracking to investigate human behaviour. However, eye-movement research is now almost a research field in its own right (see Holmqvist, Nyström, Andersson, Dewhurst, Jarodzka, & van de Weijer, 2011), and I therefore often consider myself an eye-movement researcher more than anything else. Besides this, I have also been strongly inspired by methods from psycholinguistics, especially that of combining verbal data with eye-tracking data (see Section 3.2 below). Recently, I have also started to be involved in studies in the field of cognitive neuroscience as well as dipping my toes in the waters of computational models. However, this thesis will not consider any detailed computational models, and it will only scratch the surface of the neuroscience of mental imagery.

1.2 Outline of the thesis

Chapter 2: Theoretical background. This chapter begins with a historical overview of mental-imagery research intended to serve as an introduction to the many challenges that face researchers trying to investigate mental imagery. This is followed by a review of studies of eye movements and mental imagery, describing recent attempts to explain findings from those studies. In addition, a rough overview is given of possible links between eye movements during mental imagery and the visual system, visuospatial attention, memory retrieval and the neural architecture of the brain.

Chapter 3: Methodology. This chapter introduces eye-tracking as a method and specifies how it can be used to investigate mental imagery and episodic-memory retrieval in situations where a person is looking "at nothing". It also describes the experimental set-ups used and demonstrates a novel method of using verbal data concurrently with eye-tracking data to investigate mental imagery.

Chapter 4: The investigations. This chapter describes the aims of the four papers and summarises their findings.

Chapter 5: Conclusion. This chapter discusses the findings from the four papers in the light of current theories regarding eye movements during mental imagery and episodic-memory retrieval.

Chapter 6: Applications and future directions. This chapter represents an attempt to describe how the findings from this thesis may be used in applied research and in a broader perspective. I also outline the directions in which I intend to continue my research.

Chapter 2

Theoretical background

Sensations, once experienced, modify the nervous organism, so that copies of them arise again in the mind after the original outward stimulus is gone.

William James (1890)

2.1 Mental imagery

Experiences of mental images occur in a wide variety of everyday situations. For instance, we frequently "see" images in our minds when recalling episodes from our past, when planning for future events, when deciding whether something would look good in our home or when reading an absorbing novel. This phenomenon is commonly referred to as "mental imagery" and can be defined as "the mental invention of an experience that at least in some respects resembles the experience of actually perceiving an object or an event either in conjunction with, or in the absence of, direct sensory stimulation" (Finke, 1989, p. 2).

The ability to mentally visualise objects and events has played a crucial role in the evolution of human cognition (Boyer, 2008), and it seems to influence thinking in a wide range of everyday situations. For instance, it has been demonstrated that this ability is pivotal when we remember events (Slotnick, Thompson, & Kosslyn, 2012), make creative discoveries (Ward, Finke, & Davies, 1995), construct mental models (Bower & Morrow, 1990) or solve problems (Hegarty, 2004), and it has also been shown to be important for athletes' mental practice (Olsson & Nyberg, 2010), in physical therapy (Malouin & Richards, 2009) and in psychological treatment of post-traumatic stress disorder, schizophrenia, depression and bipolar disorder (Pearson, Deeprouse, Wallace-Hadrill, Burnett Heyes, & Holmes, 2013).

In popular terms, experiences of mental imagery are often referred to as "seeing something with the mind's eye". The concept of "perceived perception" is not limited to the visual modality – we can also "hear with the mind's ear", "smell with the mind's nose", and so on – but in this thesis, mental imagery will consistently be discussed and investigated in relation to the visual modality only, unless otherwise stated.

2.1.1 Mental imagery: experience, nature and role

Even though most of us are familiar with mental-imagery experiences (for an overview of claims that some people never have such experiences, see Brewer & Schommer-Aikins,

2006), the meaning of the expression "mental imagery" is surprisingly hard to define. The co-existence of various meanings and understandings of the concept of mental imagery has caused, and continues to do so, a great deal of confusion in discussions of this concept. In an attempt to make things clearer, I have identified what I believe are the three main perspectives from which mental imagery is viewed in the scientific literature: (1) the experience of mental imagery; (2) the nature of mental imagery in the mind or brain; and (3) the role of mental imagery in cognition.

The experience of mental imagery

When viewed from the perspective of experience, as in Finke's (1989) definition quoted above (p. 16), mental imagery is characterised in terms of how we consciously experience it. Because of their inherently private quality, people's experiences are non-observable. Therefore, any reflections upon them are necessarily subjective and introspective. For this reason, investigations are typically based on people's verbal reports of their reflections on their own mental images. The first systematic investigation of such verbal reports was carried out by Galton (1880, 1883), who designed a questionnaire asking people to describe the quality of their mental-imagery experiences in terms of colours, vividness, details, shapes, distances, etc. (Galton, 1883, pp. 255–256). However, studies based on this type of introspective reports have often met with scepticism from the scientific community – and rightfully so. Indeed, findings deriving from pure introspection do not belong in a sound scientific methodology. Nevertheless, the use of systematic ratings of individual imagery experiences is accepted as a supporting method and occurs frequently in contemporary research (for an overview, see Kozhevnikov, Kosslyn, & Shephard, 2005). The collection of such ratings makes it possible to analyse mental imagery as a dependent variable. Combined with more objective methods, systematic ratings can provide valuable information about differences in how individuals acquire and process imagery information (see Paper III). This issue will be further discussed below (see Section 2.2.4).

The nature of mental imagery in the mind or brain

Influenced by cognitive science and computational models of the mind (e.g., Miller, 2003), several theorists and researchers have argued that mental imagery should not be understood in terms of experiences but rather in terms of the nature of the underlying "representations", "processes", "mental states" or "mechanisms" (e.g., Kosslyn, Thompson, & Ganis, 2006) giving rise to the imagery experience. Taking such a perspective, Kosslyn et al. (2006, p. 4) have argued that "a mental image occurs when a representation of the type created during the initial phases of perception is present but the stimulus is not actually being perceived". This conception of mental imagery concerns itself exclusively with the nature of mental imagery as such, to the exclusion of people's experience of it, and investigates it as an independent variable through behavioural and neurological output. Research on the nature of mental imagery is, however, a very complex pursuit, among other things because it may target different levels of abstraction.

To better explain this, I will refer to the three levels of Marr's (1982, pp. 24–26) seminal framework that he argued were needed to fully understand an information-processing system. Marr's first level is computational and focuses on what the system is designed to accomplish. As regards mental imagery, this level relates to its functions, i.e. to what we actually achieve by engaging in mental imagery. Marr's second level is algorithmic and focuses on the system's representations and processes, i.e. how the computational functions of the first level are accomplished. Mental-imagery research targeting this level has focused

2.1. MENTAL IMAGERY

largely on the format of the representations (Kosslyn et al., 2006; Pylyshyn, 2002), on how they are processed (Kosslyn, 1994), and how this relates to structures and processes of perception (Finke, 1989). This level is the principal arena of the “analog–propositional debate” (see Section 2.1.4 below). Finally, Marr’s third level concerns implementation and focuses on the system’s physical substrates (or hardware). At this level, the only relevant questions concern how mental imagery is physically implemented in the brain (Kosslyn et al., 2006). Typically, mental-imagery research targeting this level aims to identify the neural architecture activated by mental imagery and to compare this with neural activation during perception.

The role of mental imagery in cognition

Finally, when the perspective taken is such that the role of mental imagery is in focus, little attention is paid to our experience and to the underlying structures in the mind or brain; what is deemed interesting is instead the function of mental imagery and its effects on other cognitive operations. This perspective is common in cognitive psychology. It does not involve any claims about the nature or mechanisms of mental imagery as such, and it can be seen as representing the first level of Marr’s (1982, pp. 24–25) framework for understanding information-processing systems. Concretely, the role of mental imagery has been studied above all in relation to memory retrieval (Paivio, 1971; Slotnick, et al., 2012), but also in contexts of problem-solving (Hegarty & Kozhevnikov, 1999), decision-making (Kahneman & Tversky, 1982), learning (Glenberg, Gutierrez, Levin, Japuntich, & Kaschak, 2004), consciousness (Hesslow, 2002), creativity (Clement, 2008), design (Gero, Tversky, & Purcell, 2001) and mental practice (Olsson & Nyberg, 2010; Sevdalis, Moran, & Arora, 2013). One claim often made in current theories of cognition is that the primary function of mental imagery is to internally simulate specific events based on past experiences (Hesslow, 2012; Moulton & Kosslyn, 2009). It is suggested that such internal simulations enable us to travel mentally back and forth in time so that we may predict a range of possible outcomes.

The concept of mental imagery in this thesis

The distinction between the experience, the nature and the role of mental imagery is very important for a complete understanding of the literature on mental imagery. However, these perspectives are often not explicitly indicated, and they may be mixed up or used interchangeably in a sloppy way. As a result it is frequently difficult to determine from what viewpoint the concept of mental imagery is seen in a given case. This thesis will refer explicitly to the experience, nature (e.g. representations, processes, mechanisms) and role, respectively, of mental imagery in passages where this distinction is important, in order to minimise the risk of sowing confusion in the reader’s mind.

2.1.2 Early views on mental imagery

Reflection upon mental imagery has a very long and winding history. Indeed, this seems to be something that humans have been trying to understand for as long as they have been trying to understand human thinking. Both Plato and Aristotle regarded mental images as pivotal to human cognition. For example, Plato in the *Theaetetus* describes our memory as a wax tablet into which our senses can engrave picture-like impressions, and Aristotle in *On the Soul* claimed that the soul never thinks without a mental image. Many later philosophers of great fame, including Descartes, Kant, Hobbes and Hume,

also deemed mental imagery to be crucially important in their theories of cognition (for a detailed overview, see Thomas, 2010).

In the late 19th century, pioneers of experimental psychology such as Wilhelm Wundt and William James conducted experiments with the aim to understand the cognitive processes underlying our “mental life”. Those experiments focused to a large extent on mental-imagery experiences and relied on introspection and subjective reporting (e.g., Wundt, 1912; James, 1890). Their participants were specifically trained in the “art of introspection” and taught how to report their experiences. The findings revealed several similarities between visual perception and visual imagery, and it was suggested that mental imagery plays an important role in memory, problem-solving, emotion and creativity (e.g., Wundt, 1912; James, 1890). Wundt (1912) even claimed that these findings supported a view according to which there is no fundamental difference between visual perception and visual imagery.

In line with this claim, a famous study by C.W. Perky (1910) reported that mental-imagery experiences can be confused with visual perception. In this study, participants were to imagine an object (e.g. a banana) while gazing at a blank screen. Unbeknownst to the participant, a progressively stronger image of the object imagined was projected onto the screen. All participants believed that they were only imagining the objects even when the strength of the projected image was well above the threshold for a conscious perceptual experience. These results were interpreted as support for the strong claim that there are no differences between perceptual experiences and imagery experiences. However, in later replications and modified versions of this experiment (Segal, 1972) it has become evident that the original experiment did not actually show that perception was confused with imagery, but that performance in a visual-perception task was impaired when participants were engaged in mental imagery. Properly speaking, the famous “Perky effect” thus does not refer to confusion between visual perception and mental imagery, but to a functional interference between the processes that mediate experiences of visual perception and of mental imagery, respectively.

2.1.3 Behaviourism and cognitive science

Arising as a reaction to the use of subjective experiments involving introspection, the behaviourist paradigm came to dominate experimental psychology and the philosophy of cognition during a large part of the 20th century (at least in North America). To behaviourists, nothing was scientific unless it was observable. Psychology was no longer a science of the mind, having instead become a science of behaviour. Introspective methods were seen as completely unscientific and internal processes were deemed to lack psychological importance. Radical behaviourists such as J.B. Watson even rejected the very idea of mental-imagery experiences and wanted to banish it from the scientific discussion (Watson, 1913). Other famous behaviourists, such as B.F. Skinner, did not deny the existence of mental-imagery experiences but rejected the approach of studying mental images as internal processes, arguing instead that mental imagery should be viewed as a behaviour that is dependent on reinforcement just like any other behaviour (Skinner, 1974). As a result, when behaviourism dominated the field of experimental psychology, studies of mental imagery were more or less non-existent in the major research environments.

However, the “cognitive revolution” of the late 1950s and early 1960s ousted behaviourism from its dominant position, and the mind as an information processor became the object of study in a convergence of research efforts within experimental psychology, theoretical linguistics and artificial intelligence. This interdisciplinary research and the re-

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sultant new perspective on how to study the mind as “the software of the brain” gave birth to what is today referred to as cognitive science (for an overview, see Miller, 2003). It was at this time that the concept of “mental representation” (e.g., Kosslyn et al., 2006) became established and that mental imagery regained its importance in psychology (e.g., Neisser, 1967). By the end of the 1960s there began to appear new mental-imagery experiments that did not rely on subjective and introspective methods. The most famous ones were Allan Paivio’s investigation of mental imagery in mnemonics, where it was demonstrated that words giving rise to vivid imagery experiences were remembered better than other words (e.g., Paivio, 1971). Based on this finding, Paivio proposed his dual-coding theory (e.g., Paivio, 1971), which states that the human mind operates with a verbal code and a mental-imagery code. Dual-coding theory thus implies that human memory comprises two functionally independent stores, one of verbal memory and one of image memory, and that if, say, a word has been encoded both in verbal memory and in image memory, the probability of retrieving it is greater than if it is stored in just one code. It should be noted, though, that Paivio did not make any claims about the format of mental-imagery representations, only about the functions of mental imagery.

The 1970s and 1980s saw several key mental-imagery experiments that remain highly influential in research on the nature of mental imagery (for an overview, see Finke, 1989). This growing body of experimental research and the rise of cognitive theories assuming a computational-functionalist theory of the mind provided the backdrop to the start of the “analog–propositional debate” (e.g., Kosslyn et al., 2006; Pylyshyn, 2002).

2.1.4 The analog-propositional debate

The “analog–propositional debate” (also known as the “mental-imagery debate”) completely disregards the experiential conception of mental imagery and the role of mental imagery in cognition. It is exclusively concerned with the format of the computational representations in the brain. The crucial question is whether imagery representations are analog representations of a depictive format with intrinsic visual and spatial representational properties, or whether they are propositional representations consisting of symbolic tokens which, without inherent depictive properties, represent things in the world to which they have an arbitrary correspondence relationship.

If mental-imagery representations are analog and have a depictive format, they differ from, for instance, language. Those defending this view are not actually claiming that mental-imagery representations are full-blown pictures in the brain or exact photographs of the scenes they depict, nor that those representations necessarily have all the properties of real pictures. But they do claim that these representations share some of the inherent properties of real pictures, for instance that they have a spatial extension with spatial relationships corresponding to distances of the depicted scene, even though they may be less detailed and less intense than real pictures or scenes (e.g., Kosslyn et al., 2006). It should also be noted that few people today believe that the “inner space” of an analog representation maps one-to-one onto the scene it depicts; rather, most researchers consider the spatial properties to be more akin to functional depictions resembling arrays or matrices (Kosslyn et al., 2006, p. 12).

By contrast, if mental-imagery representations are propositional, then all of our internal representations have the same functional nature – in other words, the internal representations giving rise to mental-imagery experiences have the same format as, for instance, language (e.g., Pylyshyn, 2002). According to this view, there are no mental images or representations with a depictive format. Here it should be pointed out that

propositional representations must not (as they often are) be confused with exact linguistic descriptions. Rather, propositional representations resemble the symbolic languages used to program computers. Jerry Fodor’s (1975) “language of thought” hypothesis has been one of the most influential ideas for the supposed workings of the computational syntax of a universal mental language of this kind.

Paper I in the present thesis deals to a certain extent with the analog–propositional debate. For further details on analog and propositional formats, see Block (1983), Kosslyn et al. (2006), Pylyshyn (2002) and Thomas (2010).

Experiments in cognitive psychology

Much empirical evidence supporting the existence of analog image representations was reported in the 1970s and the 1980s (e.g., Finke, 1989; Kosslyn, 2006). It came mainly from experiments based on measures of reaction times and cleverly designed tasks. The most classic experiments are the “image scanning” studies by Kosslyn (1973) and Kosslyn, Ball, and Reiser (1978). In the study by Kosslyn et al. (1978), participants first memorised a map with seven locations. Then they closed their eyes, visualised the map and were instructed to focus their attention on one of the seven locations. Finally, they were instructed to move their attention, continuously and as quickly as possible, to another location on the map. On average, the time it took them to move between two locations was directly proportional to the distance between those locations on the actual map. Finke and Pinker (1983) extended those findings: they conducted a series of experiments where participants first inspected a random dot pattern which was then replaced with an arrow. Their task was to judge, as quickly as possible, whether the arrow was pointing at one of the previously shown dots (see Figure 1). Reaction times were found to increase linearly with the distance between the arrow and the dot to which it was pointing.

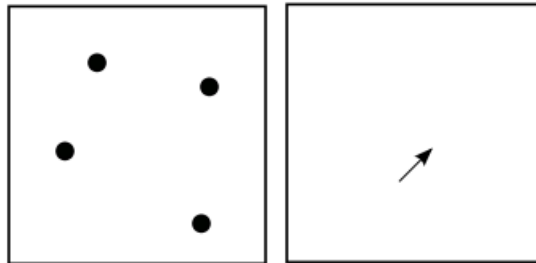


Figure 1: Example of a presentation sequence in the image-scanning studies by Finke and Pinker (1983). Participants were first shown a dot pattern (left). Then they were shown an arrow (right) and were to judge, as quickly as possible, whether it was pointing at any of the dots seen in the previously shown dot pattern.

Findings of this kind were taken as strong support for the hypothesis that mental-imagery representations have an analog format with an inherent spatial extension. Other key experiments from this time showed a similar relationship between reaction times and spatial features (for an overview, see Finke, 1989). Shepard and Metzler (1971) and Cooper and Shepard (1973) showed that the time required to perform tasks of mental rotation increases with the amount of rotation. Kosslyn (1975) demonstrated that when a person is imagining objects of different sizes, the time needed to mentally zoom in on features is shorter for large objects than for small ones. Podgorny and Shepard (1978) conducted an experiment where participants were to judge whether a probe appeared on or off an imagined block letter in a five-by-five grid. In a condition of initial visual

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perception, the letters were shown before the probe; and in an imagery-only condition, the letters came from an auditory cue visualised by participants in the grid before the probe was shown (see Figure 2). Reaction times were found to be considerably slower when the probe was close to an edge of the letter, and this effect was equally strong for both conditions.

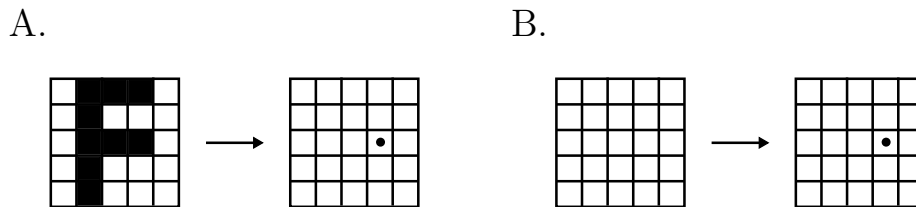


Figure 2: The experiment by Podgorny and Shepard (1978). In a visual-perception condition, participants were shown a grid containing a letter (A, left). In an imagery-only condition, they were shown an empty grid in which they were to imagine a letter based on an auditory cue (B, left). In both conditions, a probe dot (right) was displayed after a delay. Participants were to judge whether the probe was on the letter they had seen or imagined.

In the 1980s, however, this interpretation of such experiments was subjected to strong criticism, mainly to the effect that the results observed were due to experimenter-expectancy effects (Intons-Peterson, 1983) or to “tacit knowledge” (e.g., Pylyshyn, 1981, 2002), not to humans’ having imagery representations with an analog format.

Experimenter-expectancy effects and tacit knowledge

Intons-Peterson (1983) argued that participants could have behaved as they did in mental-imagery experiments because they responded to the experimenter’s expectations for their behaviour. In a series of experiments she demonstrated that, for certain aspects of the data collected, participants were indeed susceptible to experimenters’ expectations of experimental outcome. For instance, she showed that scanning times during mental-imagery tasks could depend on what the experimenter expected them to be (Intons-Peterson, 1983). This critique can be extended to data from most mental-imagery experiments. To avoid the possibility of experimenter-expectancy effects, experiments must be very carefully designed.

Another major criticism levelled at results from mental-imagery experiments is that they could be an effect of tacit knowledge (e.g., Pylyshyn, 1981, 2002) – that is, knowledge of how you “should” behave in a certain situation. In this context, Pylyshyn (e.g., 1981, 2002) has argued that participants possess tacit knowledge of how their visual system functions and therefore, when assigned a mental-imagery task, will perform an appropriate simulation of looking at stimuli. Consequently, when participants are asked to imagine a figure, they use their tacit knowledge of what it would be like to see this figure and imitate this as far as they can. For instance, in an image-scanning task such as the one studied by Kosslyn et al. (1978), participants supposedly behaved as they did because they were pretending to scan a real image. The results of mental-scanning experiments would therefore only be epiphenomenal and not related to the scanning of an internal image representation.

Tacit-knowledge explanations can, in principle, be attributed to any results taken as support for the existence of analog imagery representations.

Experiments in neuroscience

In the 1980s and 1990s, there began to appear neuroscience studies that, according to researchers such as Farah (1988) and Kosslyn (1994), were insensitive to tacit-knowledge explanations. For instance, Farah (1988) argued that in order for results due to tacit knowledge to appear in neuroscientific studies, participants would not only have to know what parts of their brains are active but also be able to alter at will their electrical activity or their blood flow in specific brain regions. This, obviously, is highly unlikely for the majority of the human population.

One major discovery which had a huge impact on subsequent vision and imagery studies was reported by Tootell, Silverman, Switkes, and De Valois (1982). They demonstrated that the primary visual cortex (V1) in monkeys is topographically organised, i.e. that the geometric structure of the retina is preserved in V1. They trained a monkey to stare at a pattern and injected the animal with a radioactive form of sugar which was absorbed by brain cells. The more active a cell was, the more sugar it absorbed. The animal was then put to death and its brain was removed for examination. The results showed very clearly that V1 had absorbed a great deal of the sugar when the pattern was observed and that the geometric structure of the pattern inspected was physically imprinted on the cortex. This study thus clearly showed that space in V1 does represent space in the outside world.

After this highly convincing evidence had been presented, proponents of analog imagery representations started to conduct brain-imaging studies of V1 in humans. Fox, Mintun, Raichle, Miezin, and Allman (1986) used positron-emission tomography (PET) to demonstrate that V1 is topographically organised and preserves the geometric structure of the retina in humans as well. Kosslyn, Thompson, Kim, and Alpert (1995) used PET to investigate V1 during mental imagery and reported activation levels varying according to image size. Le Bihan, Turner, Zeffiro, Cuenod, Jezzard, and Bonnerot (1993) used functional magnetic-resonance imaging (fMRI) and measured activation in V1 as participants were alternately inspecting and imagining patterns. Their results revealed that V1 was activated during mental imagery as well as during visual perception. Slotnick, Thompson, and Kosslyn (2005) extended those studies with an fMRI study, reporting retinotopic activation in both V1 and V2 (another part of the visual cortex). And Kosslyn, Pascual-Leone et al. (1999) used transcranial magnetic stimulation (TMS) to disrupt participants' neural activity in V1 during mental imagery, reporting that participants became slower at making judgements based on mental imagery following the application of TMS to the visual cortex. For further details on mental imagery and neural substrates, see Section 2.2.2 below.

Note that the introduction of neuroscientific studies caused the focus of the analog-propositional debate to shift from the “software” to the “hardware” of the brain. Therefore, even though our understanding of how mental imagery is related to brain activity took a large leap forward, neuroscientific experiments were actually not able to address the issue of the format of mental images (Pylyshyn, 2003), and the debate remains in the deadlock where it has been for the past forty years.

2.1.5 Embodied and enactive theories of the mind

Even though the analog-propositional debate has dominated theories and discussions regarding mental imagery, many current models of the mind do not take a computational-functionalist approach to cognition (which both sides of the analog-propositional debate do). Inspired by Gibson's (1979) ecological approach to perception, several current theorists instead support a dynamic view of the mind where modal simulations, motor processes

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and situated action underlie cognition (e.g., Barsalou, 2008; Currie, 1995; Hesslow, 2012; Spivey, 2007). In such accounts, the mind is not the software of the brain and there are no discrete representational brain states with sharp boundaries between the three components of perception, cognition and action. Instead, those components are considered to be part of a single, continuous process that naturally loops back and alters itself over time (Spivey, 2007, p. 9).

In this context, Barsalou’s theory of “grounded cognition” (Barsalou, 1999, 2008) and Thomas’s (1999, 2009) “enactive theory” have exerted a strong impact on current research into mental imagery. According to Barsalou (1999, 2008), cognition is grounded in the brain’s modality-specific systems and all concepts are represented as “perceptual symbols”. A perceptual symbol of an object is considered to be a neural simulation of the brain processes that would be involved in the actual perception of that object. It is, however, uncertain to what extent those perceptual symbols differ from the mental images of the traditional approach, and there are no established models explaining how a simulation of perception is supposed to work without analog representations.

Inspired by the concept of “active vision” from robotics, Thomas (1999) has developed a more extreme position which is referred to either as the “perceptual-activity theory” or simply as “enactive theory”. Enactive theory is strongly inspired by theories of vision that rely more on the outside world than on rich, detailed internal representations (e.g., O’Regan & Noë, 2001). Thomas (2009) denies the very existence of internal representations, arguing that seeing is not like taking a photograph, with the image file being passed on to a computer/the brain for further processing, but rather resembles the performance of a scientific test on the environment surrounding us. On this view, visual perception is not a matter of passive reception but a purposive process which asks questions about our surroundings and actively seeks out answers. Consequently, mental imagery consists of the enactment of the perceptual acts that would be carried out if the person were actually perceiving that which he or she is imagining (Thomas, 1999). Visually imagining a friend’s face would thus be to see nothing-in-particular as your friend’s face.

Barsalou (1999, 2008) and Thomas (2009) are but two of many influential theorists who highlight sensorimotor simulations and situated actions as fundamental elements of the mind in general and of mental imagery in particular. Similar ideas can, for instance, be found in Glenberg’s (1997) and Rubin’s (2006) theories of memory systems, in Hesslow’s (2002, 2012) simulation theory of consciousness and in Spivey’s (2007) theory of the continuity of mind. Embodied accounts as such should, however, not be considered as one uniform theory of the mind. There are often considerable and important differences among them. Even so, they all differ from the traditional computational view of the mind in that they favour dynamic processes over discrete brain states, highlight the importance of being actively situated in an external environment, and consider there to be no clear boundaries between action, perception and cognition. See also Parthemore and Morse (2010) for an attempt to merge representational and enactive accounts.

It should be pointed out that theories grounded in simulation and re-enactment of perception should not be confused with tacit-knowledge accounts (see Section 2.1.4), where behavioural outcomes are explained with reference to tacit knowledge of how you “should” behave in a certain situation. When seen as caused by tacit knowledge, behavioural outcomes of mental-imagery processes (e.g., image formation and image scanning) are only epiphenomenal by-products. In the embodied models of theorists such as Barsalou (1999, 2008) and Hesslow (2002, 2012), by contrast, re-enactments of perception are the most basic elements of cognition, and any processes giving rise to mental-imagery experiences are therefore functionally dependent on such mental simulations.

2.2 The perception-imagery relationship

While the predominant aim of research on mental imagery has been to determine the underlying format of the internal representations (e.g., Kosslyn et al., 2006; Pylyshyn, 2002; Thomas, 2010), there has also been a great deal of research focusing more on the similarities and differences between mental imagery and perception without making any explicit claims about the representational format as such. For instance, Finke (1985, 1989) has tried to identify general and underlying principles that are common to most mental-imagery tasks, and then to characterise those principles by reference to principles of visual perception. Farah (1988) has taken a similar approach but focused on determining whether and, if so, when visual imagery engages the same representations that are used in visual perception. Perspectives of these kinds are more or less agnostic as regards the exact format of the underlying representations, aiming instead for the systematic description of similarities between visual perception and visual-imagery representations. Finke (1986) has argued that whenever imagery and perception are found to share common neural mechanisms in the visual system, an attempt should be made to determine the lowest visual levels at which such mechanisms may be shared, suggesting that “if visual pattern perception is conceived of as involving an orderly sequence of information-processing stages ranging from the lowest to highest levels of the visual system, one might begin by trying to discover how far down in this sequence image formation can influence the underlying mechanisms”. This thesis will start from a similar perspective and investigate whether mental imagery shares mechanisms even with the low-level motor processes of eye movement.

There is much empirical evidence in favour of the view that visual perception and visual imagery share the same functions (for overviews, see Finke, 1985, 1989; Farah, 1988). For instance, it has been shown that, depending on the task, visual imagery can both facilitate visual perception (Ishai & Sagi, 1995) and interfere with it (Segal, 1972). Moreover, there is an accumulating body of research reporting that, to a large extent, visual perception and visual imagery share the same neural substrates (e.g., Kosslyn et al., 2006).

Before specifying the levels at which perception and imagery appear to share neural architecture, I will give a brief overview of the human visual system and the associated pathways in the brain (for more detailed descriptions, see Farah, 2000; Gazzaniga, Ivry & Mangun, 2008).

2.2.1 The human visual system

The human eye lets light in through the pupil, inverts the image and projects it onto the retina. The back of the retina is filled with photoreceptors called cones and rods. The rods are sensitive to low levels of light and are most useful under dim light conditions while the cones require more intense light than rods and are sensitive to the frequency of light, which is what provides us with colour vision. The cones are densely packed near the centre of the retina in a region called the fovea (which spans less than two degrees of the visual field). On the periphery of the retina, by contrast, cones are very sparsely distributed. As a result, we have full acuity only in the fovea. The separate functions of cones and rods represent the earliest step of a general design that is found throughout the human visual system. Instead of favouring either good resolution or good sensitivity to dim light, the visual system of rods and cones divides the image into two: one that favours spatial resolution and one that favours light sensitivity.

On its way to the brain, the information from each eye, still thus divided, passes through an optic nerve. Before entering the brain, the optic nerves meet and cross at the

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optic chiasm, at which point all information from the left visual field is sent to the right hemisphere of the brain and all information from the right visual field is sent to the left hemisphere.

Once inside the brain, each optic nerve divides into different pathways. The largest pathway is called the geniculostriate pathway and projects to the lateral geniculate nucleus (LGN) of the thalamus, terminating in the primary visual cortex (V1) of the occipital lobe. The image remains divided into two at this stage: magnocellular neurons carry coarse information at a high temporal resolution (at the expense of detail), while parvocellular neurons carry detailed information at a high spatial resolution (at the expense of speed).

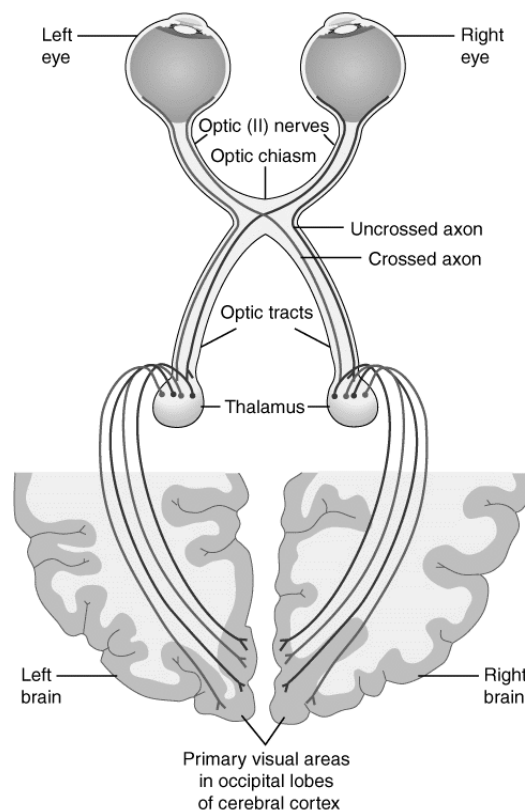


Figure 3: The primary projection pathways of the visual system. Picture from Wikimedia Commons.

When the visual signals from the geniculostriate pathway reach V1, the image still retains its retinotopic organisation. From here on, however, visual processing becomes extremely complex, continuing from V1 into the extrastriate visual areas (commonly referred to as V2, V3, V4 and V5). The exact topology of the visual cortex and the function of the cortical visual areas remain hot topics of debate (e.g., Farah, 2000; Gazzaniga et al., 2008). Still, there is much evidence that the signal is broken down into components representing features such as lines, edges, textures, colours, orientation and motion, and that specific regions of the visual cortex are dedicated to processing specific subsets of these components. For instance, V1 and V2 are sensitive to orientation and spatial resolution, V4 is sensitive to colour information and V5 (also known as MT) is sensitive to motion and directions (e.g., Farah, 2000). However, most of these regions are interconnected in complex networks. After the visual cortex, visual processing continues in two cortical pathways: the ventral stream of the inferotemporal cortex and the dorsal stream of the

parietal cortex. The ventral stream mainly processes appearance information and the dorsal stream mainly processes spatial information. See Figure 3 for an illustration of the visual system and Figure 4 for the locations of the ventral and dorsal streams.

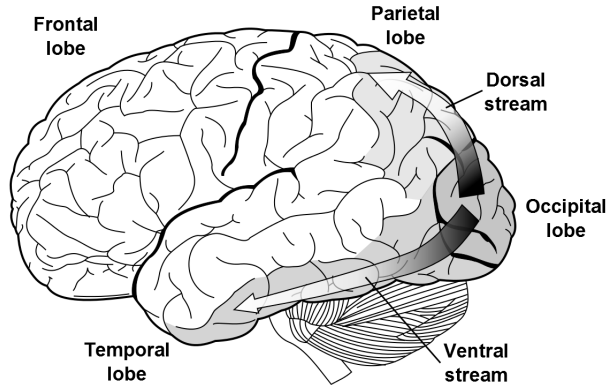


Figure 4: Two key cortical pathways: the ventral stream of the inferotemporal cortex and the dorsal stream of the parietal cortex. Picture adapted from Wikimedia Commons.

2.2.2 Mental imagery in the human visual system

In relation to the visual system, mental imagery can be seen as running visual perception “backwards” (Farah, 2000, p. 275). In rough terms, the sensations which make us experience that we are seeing something during actual perception travel “bottom-up” from retinal information via the visual cortex to the extrastriate visual areas where more abstract high-level processing takes place, whereas mental imagery involves a “top-down” journey in the opposite direction. However, there is disagreement over the issue of how far “down” in the visual system activation is triggered by mental imagery.

It has already been mentioned (Section 2.1.4) that studies have reported similar activity in V1 during imagery as during perception (e.g., Le Bihan et al., 1993; Slotnick et al., 2005). Farah, Peronnet, Gonon, and Giard (1988) used event-related potentials (ERP) to investigate the interaction between imagery and perception in occipital regions, demonstrating that imagery had a content-specific effect on ERP components subsequently to the administration of a visual stimulus within the first 200 ms of processing. Kosslyn, Thompson, and Alpert (1997) used PET, and Ganis, Thompson, and Kosslyn (2004) fMRI, to produce detailed accounts of overlapping neural activity for both imagery and perception. Their results revealed large overlaps from the frontal cortex to the occipital cortex, even though the posterior part of the brain was activated more strongly by perception than by imagery.

There are, however, contradictory findings when it comes to whether the early visual cortex is activated during mental-imagery tasks. D’Esposito, Detre, Stallcup, Alsop, Tippet, and Farah (1997) used fMRI and found no activation reaching V1 when participants were to generate mental images, and Chatterjee and Southwood (1995) reported that patients with cortical blindness could answer questions that required mental imagery. What is more, activation of V1 does not necessarily mean that this area is essential to the generation of mental images. In fact, it may well be the case that such generation is performed in associated areas and that the activation of V1 is the result of feedback connections. The claim that mental images are displayed on the primary visual cortex therefore remains controversial (e.g., Pylyshyn, 2003). However, a recent fMRI study by

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Albers, Kok, Toni, Dijkerman, and de Lange (2013) has reported convincing evidence that the early visual cortex (V1–V3) is indeed functionally involved during mental imagery.

Further evidence of how mental imagery relates to the visual system comes from studies of patients with brain damage. An early study by Bisiach and Luzzatti (1978) showed a dramatic effect: patients with left visual neglect also neglect the left side when engaging in mental imagery. Farah, Soso, and Dasheiff (1992) studied a patient before and after a surgical lesion to the occipital cortex, reporting that the reduction of the visual field due to the surgery also reduced the size of her mental images. See Farah (2000) for an overview of further studies where patients with brain damage have been reported to have similar deficits during both perception and imagery.

However, there is also conflicting evidence in the literature on brain lesions. Bartolomeo, Bachoud-Levi, de Gelder, Denes, Dalla Barba, Brugieres, and Degos (1998) described patients with associative agnosia who retained a good visual-imagery ability. Milner and Goodale (1995) investigated a patient who could not reliably distinguish circles from squares yet performed well on imagery tasks. There are also reports of patients who show imagery impairment but have intact visual perception (for an overview, see Farah, 2000).

Here a rather obvious fact should be pointed out: a complete overlap between imagery and perception is not to be expected given that it is crucial for our cognitive system to be able to distinguish the two. Experimental support for this important point has been provided by Ganis and Schendan (2008), who reported opposite signals in certain ERP components during visual perception and visual imagery, respectively. Such results are a useful reminder that we do not in fact routinely confuse visual percepts with mental images even though they engage (at least some of) the same neural substrates in the visual system.

Finally, a great deal of research has been carried out into hemispheric specialisation during mental imagery (e.g., Farah, 2000; Kosslyn, Holtzman, Farah, & Gazzaniga, 1985; Richardson, 1999) – primarily in relation to the claim, widespread in popular psychology, that the right hemisphere is associated with imagination and creative thinking while the left one is associated with logic and analytical thinking. It has been found that this claim entirely lacks empirical and scientific support (for reviews, see Ehrlichman & Barrett, 1983a; Gazzaniga, 2000; Richardson, 1999). Moreover, also contrary to this claim, there is evidence that mental-imagery generation is primarily a function of the left hemisphere (Farah, 2000, pp. 275–289; Kosslyn et al., 1985). This evidence comes not only from studies of “split-brain patients”, i.e. patients who have had their corpus callosum (which connects the two hemispheres of the brain) severed (Kosslyn et al., 1985), but also from studies of typical adults (for overviews, see Farah, 2000, pp. 275–289; Richardson, 1999, pp. 61–67). The experimental set-up used in such studies is that stimuli are shown either to the left visual field (which projects to the right hemisphere) or to the right visual field (which projects to the left hemisphere). The subsequent mental-imagery task is to generate mental images of the stimuli thus encoded. Because each stimulus to be imagined has been shown only to one of the hemispheres, performance at image generation can be measured for each hemisphere separately. However, there is also evidence against a left-hemispheric specialisation for image generation, and overall it appears that most mental-imagery processes are not lateralised but activate neural substrates in both hemispheres (for an overview, see Farah, 2000, pp. 275–289).

Object and spatial imagery

When studying the relationship between perception and imagery, it is important to distinguish the “what” aspect (identification of objects) from the “where”/“how” aspect (location and attention) of the processing of visual information (e.g., Farah, 2000). Ungerleider and Mishkin (1982) demonstrated that these two aspects are processed in two cortical systems which are anatomically distinct from and functionally independent of each other (even though more recent evidence indicates that the systems may in fact not be entirely independent of each other (e.g., Farah, 2000)). These systems are today commonly referred to as the ventral (“what”) and dorsal (“where”/“how”) streams. The ventral stream is mostly located in the temporal lobes and the dorsal stream is mostly located in the parietal lobes (see Figure 4).

Farah and her colleagues (see Farah, 2000) have studied the role of these two cortical systems in patients with damage to either the ventral or the dorsal stream performing mental-imagery tasks. They found compelling evidence that the function of these systems is similar during visual imagery and visual perception. Lesions in the ventral stream impaired performance in object-imagery tasks (imagery tasks related to appearance) but not in spatial-imagery tasks (imagery tasks related to location and attention), and lesions in the dorsal stream impaired performance in spatial-imagery tasks but not in object-imagery tasks. Consequently, imagery tasks focusing on location, spatial relationships, movement or spatial transformations mostly activate the dorsal stream, whereas imagery tasks primarily related to the processing of information about colour, shape and texture mostly activate the ventral stream.

2.2.3 Mental imagery and memory retrieval

When considering the structural equivalence between perception and imagery, it is also important to highlight the fact that the function of mental imagery is inherently associated with memory structures (Wheeler, Peterson, & Buckner, 2000) and that mental imagery has been shown to act as a critical medium for memory retrieval (Slotnick et al., 2012). One well-known mnemonic technique is the “method of loci”, which involves a person remembering items by mentally locating them at particular landmarks along a mental recreation of a familiar route (Bower, 1970; Yates, 1966). Another phenomenon of relevance in this context is the previously mentioned effect that words giving rise to vivid mental-imagery experiences are more easily remembered (Paivio, 1971; Richardson, 1999). However, in everyday life mental imagery is rarely used under such strategic control or to perform specific memory tasks. Instead it is more often intertwined with episodic-memory retrieval, which is what enables us to travel back in time mentally and simulate events of our past in great detail (Tulving, 1983). Current theories suggest that such episodic re-experiencing is based on the re-enactment of cortical processes that were active at the time of the original experience (e.g., Marr, 1971; Norman & O’Reilly, 2003). This notion is supported by a large body of research (Danker & Anderson, 2010; Kent & Lamberts, 2008; Rugg, Johnson, Park, & Uncapher, 2008; Wheeler et al., 2000) and is consistent with the view that perception and imagery are structurally equivalent (Finke, 1980) and share common neural mechanisms (Kosslyn et al., 2006; Slotnick et al., 2012). For instance, it has been demonstrated that the retrieval of memories of objects and spatial locations activates neural architecture in the ventral and dorsal streams, respectively (Khader, Knoth, Burke, Ranganath, Bien, & Rösler, 2007), and that there is a large overlap between encoding and recall in terms of the neural machinery activated (Danker & Anderson, 2010; Kent & Lamberts, 2008; Rugg, Johnson, Park, & Uncapher, 2008; Wheeler et al., 2000).

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Nevertheless, mental imagery and memory retrieval also activate separate neural correlates (Huijbers, Pennartz, Rubin, & Daselaar, 2011).

All of us are constantly reminded that our memories are often inaccurate. Sometimes we misremember specific properties or completely fail to recollect an episode. How well we succeed at remembering episodes is considered to be largely dependent on the interaction between the retrieval cues available to us and the memory traces that we have stored (e.g., Tulving, 1983). We are more successful at retrieval when there is a large overlap between the processes engaged during encoding and retrieval, respectively (Morris, Bransford, & Franks, 1977; Tulving & Thompson, 1973). This compatibility effect is supported by a vast amount of research (for a review, see Roediger & Gynn, 1996).

The function of mental imagery in memory retrieval will be considered in Paper III in this thesis while retrieval performance during episodic recollections will be specifically targeted in Paper IV.

2.2.4 Individual differences

Another important aspect to consider in studies of mental imagery and of the relationship between imagery and perception relates to differences between individuals in their abilities, preferences and expertise as well as in how they acquire and process information (e.g., Kozhevnikov, 2007). Studies of individual differences in these aspects can provide a great deal of insight into human cognition and can potentially explain conflicting results and unexpected variance.

Galton (1880) was a pioneer in individual-differences studies of mental imagery and devised a questionnaire in which participants were to evaluate, using their own words, the quality of their mental-imagery experiences. Galton used this questionnaire in some very questionable studies of differences between men and women in their “power of visual representation”, claiming that mental imagery was almost an unknown phenomenon among men in the scientific community (Galton, 1880). Even so, Galton’s studies showed clearly that there was considerable diversity in mental-imagery experiences among individuals. This inspired Betts (1909) to develop the first quantitative questionnaire on mental imagery (QMI), which was later revised by Sheehan (1967) into a shorter version which is widely used today. Paivio (1971) designed another, very influential questionnaire where participants are categorised as either verbalisers or visualisers. Building on Bett’s and Paivio’s work, several other researchers have since developed improved tests to investigate individual differences in the processing of visual, spatial and verbal information during imagery tasks (for overviews, see Kozhevnikov, et. al, 2005; Richardson, 1999). However, the basis for the design of most of these tests has not been the neural architecture of the human brain but rather intuition and assumptions deriving from subjective experiences. As a result, it is often difficult to tell what is actually measured by many of these tests, and in particular to determine whether the results are related to spatial imagery in the dorsal stream or to object imagery in the ventral stream.

For this reason, Kozhevnikov et al. (2005) undertook a detailed investigation and evaluated several tests of individual differences. One of their findings was that the widely used Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973b) mostly measures object imagery, not spatial imagery. They also found that individuals tend to encode and process imagery information using either spatial imagery or object imagery: those who are oriented towards object imagery encode images more globally as single units and process them more holistically, whereas those who are oriented towards spatial imagery encode and process images more analytically – one part at a time – and use spatial relationships to

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arrange and analyse image components. In a follow-up study, Kozhevnikov, Blazhenkova, and Becker (2010) have also shown that there is a trade-off between object-imagery and spatial-imagery ability. They propose that the reason for this trade-off may be that both object-imagery and spatial-imagery processing call upon resources with limited capacity, such as visual attention. It is therefore possible that, during the functional integration of the dorsal and ventral streams in early childhood, either object-imagery ability or spatial-imagery ability develops at the expense of the other. For example, a child with strong overall spatial-processing resources might develop a preference for attending to locations and spatial relationships at the expense of objects and their features. In support of this view, Kozhevnikov et al. (2010) also reported that participants working in the visual-arts field had above-average object-imagery skills and below-average spatial-imagery skills, while the opposite pattern was found for scientists.

Paper II in this thesis focuses on individual differences and specifically targets abilities and preferences as regards object imagery and spatial imagery.

2.3 Eye movements and mental imagery

Several studies have shown that, in most situations, the direction of the human gaze can be used as a reliable proxy for the orientation of spatial attention (e.g., Schneider & Deubel 1995; Theeuwes, Kramer, Hahn, & Irwin, 1998). However, it has also been demonstrated that attention can be re-oriented “covertly” without overt eye movements (e.g., Posner, 1980), and it has been suggested that covert attention shifts have evolved as preparatory mechanisms for overt attention shifts (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Sheliga, Riggio, & Rizzolatti, 1994). For instance, Henderson, Pollatsek, and Rayner (1989) have shown that the direction of attention to a certain location precedes eye movement to that location, and Posner (1980) described covert attention as a mental “spotlight” preceding overt attention. Nevertheless, situations where attention is re-oriented covertly without eye movements are mostly found in the laboratory – in conjunction with stimuli designed for this exact purpose and/or specific task instructions (e.g., Posner, 1980) – or in certain real-life situations where we make a conscious effort to attend to something without moving our eyes (e.g. while spying on someone). In everyday life, attention shifts are usually accompanied by the corresponding eye movements (e.g., Shepherd, Findlay, & Hockey, 1986). Thus, the direction of the gaze is often used – both in research and in everyday life – as an approximation of what information our attention is focused on (see Holmqvist et al., 2011). This is commonly referred to as the “eye–mind hypothesis” (Just & Carpenter, 1980).

However, we only see with full resolution within about two degrees of visual angle. This roughly corresponds to a person’s thumbnail at arm’s length. For this reason, eye movements are almost always essential for our perception of a scene. By shifting our gaze to different regions of a scene, we create the illusion of seeing the entire scene in high resolution. In this procedure, our eye movements are driven by either “bottom-up” factors such as more salient regions in the scene, or “top-down” factors such as our knowledge of how to look at a certain type of scene. However, the extent to which this procedure is driven by bottom-up and top-down factors, respectively, is a controversial issue (e.g., Underwood, Foulsham, Loon, Humphrey, & Boyce, 2006; Henderson & Ferreira, 2004; Holmqvist et al., 2011).

When we engage in mental imagery and memory retrieval, there is usually no relevant external information to look at. Consequently, there are no bottom-up factors to drive eye movements and no visual scene whose inspection can be guided by top-down factors. It would thus seem pointless to accompany attention shifts with eye movements. Nevertheless, as I have described above, many parts of the visual system are similarly activated during imagery as during perception, and it has been found not only that spontaneous eye movements frequently occur when a person is engaged in a mental-imagery task but also that those eye movements closely reflect the content and spatial layout of an imagined scene (e.g., Brandt & Stark, 1997; Laeng & Teodorescu, 2002). Could it be that the top-down processes that operate when we are inspecting actual scenes are also activated when we are visualising scenes from memory? Then the eye movements observed during mental imagery could be linked to cognitive processes that cause us to engage in mental imagery and to processes used to orient attention when visuospatial information is being maintained and manipulated in working memory.

2.3.1 Eye-tracking studies of mental imagery

The empirical study of eye movements during visual imagery has rather a long history. Early studies observed a large amount of eye-movement activity during mental imagery

(Moore, 1903; Perky, 1910; Jacobson, 1932), and it was reported that this effect varied between different stimuli (Clark, 1916), among individuals (Stoy, 1930) and with the estimated level of vividness (Goldthwait, 1933). Totten (1935) even used a photographic technique to measure eye movements, arguing that eye movements frequently correspond to the shape of visualised objects.

However, conflicting results from later studies, which focused on either eye-movement rates (EMRs) or electro-oculograms (EOGs), brought the link between eye movements and visual imagery into question. Some studies reported that mental imagery was associated with a high EMR (Brown, 1968; Lorens & Darrow, 1962) while others reported the opposite pattern (Antrobus, Antrobus & Singer, 1964; Hale & Simpson, 1970; Marks, 1973a). Further, several studies reported that non-visuospatial mental activity (such as solving arithmetic problems and performing verbal-linguistic tasks) was more likely to induce ocular movements than visual-imagery tasks (Hiscock & Bergstrom, 1981; Ehrlichman & Barrett, 1983b; Bergstrom & Hiscock, 1988; Weiner & Ehrlichman, 1976). Weiner and Ehrlichman (1976) argued that such results indicate that eye movements are actually inhibited during visuospatial imagery in order to screen out potentially interfering information from visual and motor input. It should be kept in mind, however, that those studies only measured EMRs and that some studies using EOGs did indeed find potential support for spatial scanning during mental imagery (Deckert, 1964; Hall, 1974; Janssen & Nodine, 1974; Zikmund, 1972).

It should be noted that the methods used – EMR measurement and EOGs – were not capable of exact determination of the orientation of the gaze nor the direction of eye movements. Furthermore, in the case of several studies, the means used to engage participants in non-visuospatial activity versus visuospatial imagery are open to criticism – it can be questioned to what extent the tasks and stimuli used actually had the intended effect. Here are a few examples. To elicit visuospatial processing, participants were asked to form a mental image while answering the question “If you are the minister at a wedding, on which side of you does the bride stand?” (Weiner & Ehrlichman, 1976) or “Which way is the beaver facing on the tail of a nickel [Canadian five-cent coin]?” (Bergstrom & Hiscock, 1988). To elicit linguistic and conceptual processing, participants were asked to solve the following three-term series problem: “Jim is better than Ted; Ted is better than Bob; who is best?” (Weiner & Ehrlichman, 1976) or to determine the meaning of the saying: “while the cat is away the mice will play” (Bergstrom & Hiscock, 1988). Here it must be pointed out that the last two examples do not encourage participants to form mental images as such, but they are still likely to have that effect in practice, considering that studies of mental-model construction have established that relational reasoning frequently induces participants to generate a mental image and that participants’ experience often involves being able to “see” the solution by inspecting such an image (for a review, see Goodwin & Johnson-Laird, 2005). To this should be added that it has been demonstrated that figurative and metaphorical language is likely to activate visuospatial image schemas (Bergen, Lindsay, Matlock, & Narayanan, 2007; Matlock, 2004; Richardson, Spivey, Barsalou, & McRae, 2003).

Related research has also long been carried out into rapid eye movements (REMs) during sleep. It was hypothesised early on that the direction of REMs corresponds to spatial relationships from ongoing dreams (e.g., Dement & Kleitman, 1957; Ladd, 1892). At the time, some studies supported this claim (Dement, 1964; Herman, Barker, & Roffwarg, 1983) while others did not (Jacobs, Feldman, & Bender, 1972; Moskowitz & Berger, 1969). The relationship between REMs and dream content remains a controversial issue to this day, even though recent studies using more elaborate techniques have found compelling ev-

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idence that REMs frequently correspond to spatial information in dreams (Doricchi, Iaria, Silvetti, Figliozzi, & Siegler, 2007; Sprenger, Lappe-Osthege, Talamo, Gais, Kimming, & Helmchen, 2010).

Finally, it is worth mentioning that eye movements have also been the subject of mental-imagery research for reasons other than the possibility that they may reflect the visualised content as such. For instance, in reaction-time experiments such as the one with arrows pointing at previous dots carried out by Finke and Pinker (1983) that was described in Section 2.1.4, researchers have been concerned that the effects reported could be attributed to eye movements instead of the internal processing of a mental image (Finke, 1985, 1989, pp. 54–55). For example, participants could have been looking at different parts of the stimulus presented, and since eye movements take time to execute, the reported reaction-time effects could have been a consequence of how the participants moved their eyes over the stimulus rather than evidence of mental scanning taking place (Finke, 1985). However, recent mental-scanning experiments have used a more careful design and have therefore been better equipped to control for eye movements. It appears to be the case that eye movements as such cannot explain reaction-time effects during mental-scanning tasks (Borst & Kosslyn, 2008, 2010). Even so, to my knowledge no studies have yet involved a detailed investigation of the impact of eye movements on the tasks that were used in the classic mental-scanning experiments (e.g., Kosslyn et al., 1978; Finke & Pinker, 1983). Still, as will be apparent in this thesis, eye movements during mental imagery should not be seen as a potential problem which might interfere with predicted results. On the contrary, they are inherently connected with the formation and scanning of mental images.

Visual elicitation

Since the late 1990s, several studies have been carried out using more sophisticated eye-tracking techniques than EMR measurement and EOGs. Their findings include that spontaneous eye movements do occur during visual imagery and that these eye movements closely reflect the content and spatial relationships of the original picture or scene. The first of these studies, and arguably the most influential one, was performed by Brandt and Stark (1997). Their participants were first shown a simple visual grid pattern that they were told to memorise. Shortly afterwards they were asked to imagine that pattern. The unique scanpaths established during the viewing of the grid pattern spontaneously reappeared when the participants later imagined the same pattern. Similar findings were made by Holsanova, Hedberg, and Nilsson (1999), who reported striking similarities between participants' eye-movement patterns when they were looking at a scene and when they were later looking at a whiteboard and describing this scene from memory. Laeng and Teodorescu (2001) replicated the study by Brandt and Stark (1997) and also found that participants who fixed their gaze centrally while perceiving a scene did the same, spontaneously, during the imagery phase.

Spivey and Geng (2001, Experiment 2) divided their display into four quadrants. Their participants were first shown four simple objects, one in each quadrant. In the subsequent recall phase, one of the objects disappeared and the participants were asked a question about the colour, shape or texture of the now-absent object. The results revealed that, while answering this question, participants were very likely to look at the region of the display where the object had originally been located. Comparable results have been demonstrated for three- to four-year-old children (Martarelli & Mast, 2011) and for adults one week after the original encoding (Martarelli & Mast, 2013).

A similar eye-movement effect has also been reported by Altmann (2004) in a blank-screen version of the “visual world” paradigm (e.g., Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995). In this study, participants looked at a set of four objects, which were then replaced by a blank screen. When the participants were listening to sentences discussing the objects they had seen, their gaze moved to the locations where the respective objects had been shown. Comparable results have been reported by Knoeferle and Crocker (2007) and by Altman and Kamide (2009). In addition, Altmann (2004) showed that the temporal latency between the provision of linguistic information and eye movements towards locations in the visual world was largely the same for “absent objects” on a blank screen and objects that were still present.

Paper I in this thesis demonstrated that spontaneous eye movements “to nothing” occur during recall even when a more complex stimulus (a detailed picture with several objects and agents) is used and that this effect is present even in complete darkness. Since Paper I was first published in 2006, comparable results have been reported by others (Liman & Zangemeister, 2012; Humphrey & Underwood, 2008, 2011; Zangemeister & Liman, 2007) and it has been demonstrated that scanpaths reflecting mental imagery of real-world scenes appear even when recall is performed two days after the original encoding (Humphrey & Underwood, 2008).

Verbal elicitation

All of the above-mentioned studies of eye movements “to nothing” involved a prior encoding phase. A different approach was taken by Demarais and Cohen (1998), who demonstrated that participants who were solving spoken syllogism problems containing the words “left” and “right” exhibited more horizontal eye movements while syllogism problems containing “above” and “below” elicited more vertical eye movements. In this case, there was no encoding phase with visual scene information; instead, a mental model (Bower & Morrow, 1990) of a scene was generated and continuously updated in the participants’ minds based on linguistic input and on participants’ prior knowledge about objects and spatial relationships, ultimately deriving from the way we structure our environment semantically. Spivey and Geng (2001, Experiment 1) corroborated these results by showing that participants who were listening to a scene description tended to make eye movements in the directions indicated within the overall structure of the scene being described, and Spivey, Tyler, Richardson, and Young (2000) demonstrated that this effect was present even when participants had their eyes closed. Comparable results have been demonstrated for participants who were visualising cities and regions on a map of France from long-term memory (Bourlon, Oliviero, Wattiez, Pouget, & Bartolomeo, 2011; Fourtassi, Hajjioui, Urquizar, Rossetti, Rode, & Pisella, 2013). In Paper I in this thesis, those earlier studies were extended through use of complex, detailed scene descriptions involving many objects and clear spatial relationships.

Richardson and different colleagues (Richardson & Spivey, 2000; Richardson & Kirkham, 2004) have investigated eye movements to blank spaces for multimodal events using both verbal and visual elicitation. However, mental imagery as such was not investigated in those studies. Richardson and Spivey (2000) divided their screen into four segments and their participants watched four films showing talking heads or four animated objects synchronised with spoken statements, with each film shown in a different segment. Richardson and Kirkham (2004) had their participants look at animated objects, synchronised with spoken statements, shown on the left-hand or right-hand side of the screen. In the subsequent recall phase, participants in both of these studies faced an empty display and were asked to give a binary answer (“yes”/“no” or “true”/“false”) to statements re-

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lating to spoken information that had been provided in the preceding encoding phase. It turned out that participants were likely to make eye movements towards the segment that had previously been associated with spoken information of relevance to a given statement. Moreover, Richardson and Kirkham (2004) have also shown a similar effect for 6-month-olds. However, Scholz, Melhorn, Bocklisch, and Krems (2011) have shown that the extent of such eye movements to blank spaces diminishes with practice. In their study, the overall design of Richardson and Spivey (2000) was replicated, i.e. spoken descriptions were associated, in an encoding phase, with one of the four quadrants of the screen and participants were then, in a subsequent recall phase, to answer “yes” or “no” to statements relating to those descriptions. Critically, both encoding and recall were repeated in a second and a third set of trials. The results revealed that the extent of eye movements to blank spaces decreased with practice across trials.

It should be noted, however, that neither of those studies investigated whether the eye-movement effect (or its weakening with practice) is equally strong for verbal and visual elicitation, which was one of the main aims of Paper I in this thesis.

Memory retrieval

Some of the above-mentioned studies have also investigated eye movements to blank spaces in relation to memory-retrieval performance. Laeng & Teodorescu (2002) reported that the correlation between eye-movement patterns at encoding and recall, respectively, predicted retrieval accuracy. Moreover, they also showed that participants who had been free to explore the pattern during the perception phase but were required to maintain central fixation during the imagery phase exhibited a decreased ability to recall the pattern. In contrast to those results, however, several of the other above-mentioned studies did not find any apparent memory-facilitation effect of eye movements to blank spaces (Hoover & Richardson, 2008; Matarelli & Mast, 2013; Richardson & Kirkham, 2004; Richardson & Spivey, 2000; Spivey & Geng, 2001). It should be pointed out, however, that there are large differences in design between those studies and the one by Laeng and Teodorescu (2002) (see above) and that – except in the case of the study by Matarelli and Mast (2013) – the recall task depended only to a small extent, or not at all, on visuospatial information from the encoding phase.

Recent studies on recognition memory have demonstrated that recognition of scenes and faces may improve when participants look at the same features of the stimuli during initial encoding and during a subsequent recognition test (Foulsham & Kingstone, 2013; Holm & Mäntylä, 2007; Mäntylä & Holm, 2006), and Mäntylä and Holm (2006) reported decreased performance in a face-recognition task when eye movements were restricted either during encoding or during the recognition test. Further, Hollingworth (2006) has shown that memory of the visual properties of an object improves when the object is presented, during a recognition test, at its original location and in the same context where it was originally encoded.

What is more, related research on visuospatial working memory has demonstrated that performance on tests where participants are to memorise the location of dots can be enhanced by eye movements that “rehearse” the original dot locations during a retention interval between encoding and recall (Brockmole & Irwin, 2005; Tremblay Saint-Aubin, & Jalbert, 2006). However, it has also been shown that covert shifts of attention are sufficient to achieve this effect, meaning that accompanying eye movements are not necessary (Godijn & Theeuwes, 2012).

The relationship between looking “at nothing” and memory retrieval is investigated in Paper III in this thesis and is specifically targeted in Paper IV.

2.4 Attention, eye movements and the brain

In this section, I will make an attempt to link eye movements during mental imagery to theories of visuospatial attention. I will also give a general overview of how the processes concerned may be connected to attentional and oculomotor mechanisms in the brain.

2.4.1 Visuospatial attention and working memory

Our attentional system has limited capacity and can only process a certain amount of information at any given time. The process of maintaining and manipulating relevant information for brief periods of time is often referred to as our “working memory”. For instance, the seminal model of working memory developed by Baddeley (1986) consists of two independent buffers and a central executive. One buffer processes visuospatial information (this buffer is often referred to as the “visuospatial sketchpad”) and the other processes verbal information (this is often referred to as the “phonological loop”). The central executive manages information in and between the buffers. The ability to control the central executive is often referred to as “working-memory capacity”. Since the visuospatial buffer processes visuospatial information that is no longer available in the outside world, it is essential when we engage in mental imagery. As part of his arguments in favour of analog representations, Kosslyn (1980, 1994) has developed a detailed and very influential model of how mental images are generated and manipulated in such a visuospatial buffer (referred to as the “visual buffer” in his model). However, recent research uses many different models of working memory that do not rely on domain-specific buffers (for a review, see Conway, Kane, Bunting, Hambrick, Wilhelm, & Engle, 2005). Such models tend to focus more on the control systems that select and inhibit information based on a domain-general capability of activating information from long-term memory. On this view, the executive function of working memory is not a simple gate-keeper between specific information buffers. Instead, it can be conceptualised as a dynamic filtering mechanism (Shimamura, 2000) which is basically the same as the ability to execute and control attention (Corbetta & Shulman, 2002; Engle, 2002). Consistently with this view, a close relationship has been shown to exist between the ability to control eye movements and working-memory capacity (Kane, Bleckley, Conway, & Engle, 2001).

In line with this, a close link between visuospatial attention and the maintenance of information in working memory has been reported in several studies (for an overview, see Theeuwes, Belopolsky, & Olivers, 2009). For instance, Awh and Jonides (2001) demonstrated that maintaining a location in working memory facilitates the processing of information to be found at that location in a similar manner as attending to a specific location in the outside world improves the processing of information to be found at that location. Theeuwes et al. (2009) have argued that the generation of mental images is identical to the maintenance of a location in visuospatial working memory, and that the scanning of a scene maintained in working memory occurs in a similar manner as the scanning of an actual scene. In support of this view, Postle, Idzikowski, Della Sala, Logie, and Baddeley (2006) have shown that the performance of a mental-imagery task is impaired by the concurrent performance of an object-tracking task, suggesting that eye movements can disrupt visuospatial working memory. Further, it has been suggested that shifts of spatial attention are by-products or manifestations of the preparation of eye movements (e.g., Deubel & Schneider, 1996; Irwin & Gordon, 1998; Theeuwes, et al., 2005). This would make the process of retrieving a location from memory identical to the process of programming an eye movement to that location. Imagining a scene would then consist in making several attention shifts towards remembered locations in that scene and would

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thus naturally generate corresponding activity in the oculomotor system (Theeuwes et al., 2009). This view is strongly consistent with embodied models of the mind, where perception, cognition and motor actions are seen as forming a single, continuous process (Spivey, 2007).

To sum up, there appears to be a strong link between working memory, visuospatial attention and eye movements. This might explain why eye movements take place in a similar manner during visual imaging as during the direction of visual attention towards locations in the outside world.

To provide a basis for subsequent attempts to identify the level or levels at which the link between eye movements, visuospatial attention and mental imagery is to be found, an outline description of relevant attentional and oculomotor mechanisms in the brain will be given in the following section (for more detailed overviews, see Corbetta & Shulman, 1998; Findlay & Gilchrist, 2003; Bisley & Goldberg, 2010; Kravitz, Saleem, Baker, & Mishkin, 2011).

2.4.2 The oculomotor system

Visual information from the outside world and our internal goals are constantly competing for access to the systems that control visuospatial orientation and eye movements. One component of the brain which is critically important for guiding orientation and directing eye movements is the superior colliculus (SC). The SC resides in the midbrain and initiates rapid motor-orientation movements such as eye movements (for a detailed description, see White & Munoz, 2011). The SC is integrated with the oculomotor cortex in both the frontal and the parietal lobes (via the basal ganglia as well as the medial dorsal (MD) and pulvinar nucleus of the thalamus). It is generally assumed that the frontal lobe is associated with conscious, top-down processing whereas the parietal lobe is more associated with unconscious, bottom-up processing (e.g., Gazzaniga et al., 2008). There is much empirical evidence that the frontal eye fields (FEF) are the primary regions in the frontal lobe related to oculomotor control and that the lateral intraparietal area (LIP) is a key structure in the parietal lobe for the guidance of visuospatial attention and eye movements (Bisley & Goldberg, 2010; Johnston & Everling, 2011; Paré & Dorris, 2011; Rafal, 2006).

Large part of the SC–parietal network bypasses the visual cortex and is older in evolutionary terms than the main visual pathways (described in Section 2.2.1). This entails that a great deal of eye and attentional guidance never reaches our conscious awareness. However, the SC is also strongly associated with the main visual pathways. Among other things, it has been shown to be involved in a network which mediates cortical excitability in the visual cortex as a function of selective attention (e.g., Gazzaniga et al., 2008). See Figure 5 for a schematic framework of the primary pathways relating to guidance and control of eye movements.

2.4.3 Mental imagery in the oculomotor system

As described in previous sections, mental imagery draws largely on the same neural architecture as visual perception. Consequently, many of the networks involved in the visual pathways are also activated during mental imagery. Since there is no visual input to be processed during mental imagery, it is completely driven by top-down processing, which requires the integration of cognitive control, attention and information from memory to “generate” what we experience as a mental image. While the existence of a close link

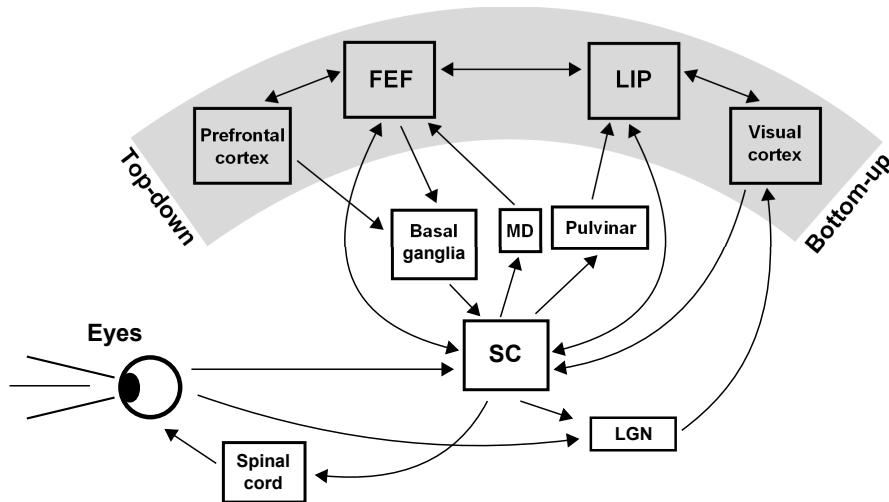


Figure 5: The primary pathways relating to guidance and control of eye movements.

between the cortical pathways involved in mental imagery and the regions involved in visuospatial attention, working memory and eye movements is well documented, the nature of the functional interactions is an issue of debate (cf. Bisley & Goldberg, 2010; Corbetta & Shulman, 1998; Findlay & Gilchrist, 2003; Kravitz, et al., 2011; Theeuwes, et al., 2009).

In an influential model of the generation of saccades (the saccade is one of the most common types of eye movement, occurring when the gaze is shifted from one location to another; see Section 3.1 for further information), Findlay and Walker (1999) have outlined a hierarchy of processing levels for when and where the eyes move when we act upon the world. The lower levels include reflexive responses to visual events in the periphery, movement decisions generated in a “motor map” of the SC, and the motor execution itself. The higher levels include voluntary movements that are under strategic control and automated selection that is driven by visual saliency and learned behaviours. For obvious reasons, eye movements during mental imagery trace their origin to the higher levels of this framework. However, since such eye movements cannot be driven by salient features in the outside world and do not appear to be driven by voluntary strategies, their nature appears to reside in a borderland which is not really explained by the framework drawn up by Findlay and Walker (1999), nor by other current models of saccade generation (for an overview, see Kowler, 2011).

Nevertheless, there is converging evidence that structures in the parietal cortex around the intraparietal sulcus (IPS) form a nexus that integrates top-down and bottom-up guidance for both attention and eye movements (Bisley & Goldberg, 2010). One of the most researched parts of those structures is the LIP area, which is part of the dorsal pathway and highly interconnected with the collicular networks described above. It has been argued that neurons in the LIP act as a “priority map” where both the spatial allocation of attention and eye movements are decided on a winner-takes-all basis (Bisley & Goldberg, 2010). This priority map combines bottom-up inputs, such as visually salient information, with top-down signals that are driven by internal goals. Depending on behavioural priorities, selective and inhibitory activations create a peak in the priority map which is used to target saccades and to guide visual attention.

The generation of mental images is clearly top-down driven in some sense, but it is not known to what extent the associated eye movements are automatically triggered or under some sort of cognitive control, nor to what extent those eye movements are

2.4. ATTENTION, EYE MOVEMENTS AND THE BRAIN

related to external and/or internal information (cf. Ferreira, Apel, & Henderson, 2008; Richardson, Altmann, Spivey, & Hoover, 2009). However, since the LIP appears to be a nexus for much of this information, it is likely to be critically involved. What is more, it has been demonstrated that the LIP (and adjacent structures) is of key importance for different sub-pathways of the dorsal stream that are associated with spatial working memory, visually guided action and navigation, and that it is linked to critical structures of episodic memory and visuospatial processing in the precuneus, medial temporal lobe and hippocampus (Kravitz, et al., 2011).

While this very broad outline of visuospatial attention and the oculomotor system does not answer the question of exactly how and why eye movements are related to mental imagery, it adds further support to the hypothesis that working memory, visuospatial attention and the oculomotor system are highly interconnected in a way which might cause eye movements to take place in a similar manner during mental imagery as when we act upon the outside world.

2.5 Theories of eye movements during mental imagery

In previous sections I have reviewed studies of eye movements during mental imagery, and I have also tried to explain in what way such eye movements could be linked to mechanisms of visuospatial attention and oculomotor control. However, those explanations have mostly focused on structural frameworks and have not specifically considered the issue of whether, and if so how, eye movements are functionally associated with mental imagery and episodic recollection.

In this section I will describe theories making more explicit claims about how eye movements are related to mental imagery and/or the phenomenon of looking “at nothing”, and I will outline the functional predictions that can be made on the basis of those theories. It is important to keep in mind that these theories have not been developed as alternatives to each other and that they should therefore not be seen as strictly exclusive and differential when compared. In fact, they may occasionally complement each other more than anything else. Even so, there are several important differences among them that enable us to determine which of them represents the best fit with the most critical aspects of the phenomenon under study.

2.5.1 Scanpath theory

Neisser (1967) argued that eye movements – or the processes driving them – are actively associated with the construction of a visual image, and Hebb (1968) suggested that eye movements are necessary to assemble and organise “part-images” into a whole visualised image. This view, where eye movements have a significant and functional role during visual imagery, was strongly supported by the findings of Brandt and Stark (1997), who reported that spontaneous eye movements occurred in participants who were looking at a blank screen during visual imagery and that the scanpaths of those eye movements closely reflected the content of the stimuli previously presented to the participants (six-by-six black-and-white grid patterns). The theoretical framework for the eye-movement comparisons made in that study originated from the “scanpath theory” developed by Noton and Stark (1971a, 1971b), which assumes that eye movements during imagery are necessary and predicts that their scanpath should follow the same sequential order as during the actual perception of the scene being imagined. The underlying theoretical assumption built on the idea that eye movements reflect the construction or scanning of analog representations present in a “visual buffer” (Kosslyn, 1994; 2006) of working memory. Eye movements would thus reflect the process of activating and arranging part-images of a scene into their proper locations and would, by its similarity to visual perception, create the illusion of “seeing” this scene as a whole. Kosslyn, Cave, Provost, and Von Gierke (1988) argued that image generation in the visual buffer is processed sequentially, and Brandt and Stark (1997) suggested that eye movements are an important tool in this process and that they might be used by the brain to construct images. Such an interpretation has been supported by Zangemeister and different colleagues (Gbadamosi & Zangemeister, 2001; Liman & Zangemeister, 2012; Zangemeister & Liman, 2007).

Other findings in support of scanpath theory were made by Laeng and Teodorescu (2002), who reported that the correlation between eye-movement patterns at encoding and recall predicted accuracy in retrieval performance, and that participants who first inspected visual stimuli and were then instructed to maintain central fixation in the subsequent recall phase were impaired in their memory performance compared with a

2.5. THEORIES OF EYE MOVEMENTS DURING MENTAL IMAGERY

group who were free to move their eyes during both encoding and recall. The same study also revealed that another group of participants who were instructed to maintain their gaze in the centre of the screen while encoding the visual stimuli would spontaneously maintain their gaze centrally during the subsequent recall phase as well. Based on these results, the authors argued that eye movements are stored along with a visual representation of the scene and are used as spatial markers to properly arrange the parts of a mental image. They concluded that eye movements during mental imagery are re-enactments of perception and have a necessary and functional role in “constructing” the mental image. This interpretation was also largely supported by Mast and Kosslyn (2002).

Predictions: Scanpath theory predicts that eye movements during the recollection of a scene will be similar to eye movements during the original encoding of that scene, and that performance at memory retrieval will be directly dependent upon the compatibility of scanpaths from encoding and recall, respectively. As regards visualisations generated from long-term memory without a preceding encoding phase, it is unclear what scanpath theory would predict. This is because this theory pre-supposes an encoding–recall procedure and was originally developed on the basis of experiments of scene recognition (Noton & Stark, 1971a, 1971b).

2.5.2 Spatial indexes

One common criticism of scanpath theory and similar accounts is based on the claim that eye movements during mental imagery do not reflect analog representations in a visual buffer but merely show how we use our environment as an external memory store (e.g., O’Regan & Noö, 2001). On this view, the eyes “leave behind” deictic pointers or spatial indexes in the outside world (Ballard, Hayhoe, Pook, & Rao, 1997). The “scanning” of a visualised image would then be accomplished by binding the objects imagined onto actual visual features in the world. Pylyshyn (2002) uses the term “visual index” for the mechanism used to bind imagined objects to perceived ones. On this theory, the “objects” in the participants’ memory are associated with actual positions in the visual environment, including the whiteboard, where slight visual features on the board and in the surrounding environment serve as visual indexes. Thinking that something is at a certain location then amounts to no more than thinking, “this is where I imagine X to be located” (Pylyshyn, 2002, p. 22). Such association requires no inner space with analog representations, only the binding of active memory objects to real objects. Consequently, the eyes would simply move to look at the position in the real world which was associated with the currently active propositional object. Visual indexes thus make the existence of an inner space unnecessary as far as eye movements are concerned.

Predictions: An account based on visual indexes predicts that eye movements will correspond to the spatial layout of an imagined scene if there is enough visual information for imagined objects to be associated with. Consequently, in a recall environment characterised by complete darkness, eye movements will not correspond to positions from an imagined scene. Visual-index theory does not make any explicit claims about retrieval performance, but it is plausible to assume that revisiting locations associated with the information to be retrieved could enhance memory performance in the spatial domain, but not in the content domain.

Pylyshyn’s visual indexes are not the only idea based on the assumption that we may use the world as an external memory store by looking at blank spaces in it. For instance, Richardson et al. (2009) have pointed out that the existence of spatial indexing does not necessarily mean that the external memory store is the only memory store available, and Ballard et al. (1997) use deictic pointers more as memory support than as an exclusive explanation in their account of information processing. On their view, positions in the outside world are used as memory traces of an observed scene, and looking at points in this external memory store is a way to relieve the cognitive demands on working memory. However, internal representations can still account for an important part of the memory traces activated during mental-imagery tasks and it is possible that the physical act of moving the eyes could in itself have a supporting function. However, the extent to which such spatial indexes are driven by external memories and by internal representations, respectively, has been a debated issue (cf. Ferreria et al., 2008; Richardson et al., 2009).

Predictions: A spatial-indexing account of this second type predicts that eye movements will often correspond to directions and positions of an imagined scene, but it also predicts that there will be a great deal of variability in the eye-movement effect due to individual differences and to differences in cognitive loads. The effect of looking “at nothing” will also be more flexible in an account of this type. Memory retrieval is likely to be enhanced, but this does not necessarily have to be the case. Again, this largely depends on the task given and on the individuals’ need to relieve cognitive demand on working memory.

2.5.3 Simulation theory and enactive theory

There are also explanations deriving from accounts where imagery experiences are not primarily considered to rely on the format of image representations, but where it is instead assumed that perception can be internally simulated by activating the necessary regions of the brain (Hesslow, 2002; 2012).

As mentioned in Section 2.1.5, Thomas has challenged the representational view of mental imagery, suggesting that instead of storing images we store a continually updated and refined set of procedures or schemas that specify how to direct our attention in different situations (Thomas, 1999, 2009). On this view, a perceptual experience consists of an ongoing, schema-guided, perceptual exploration of the environment. Imagery, then, is the re-enactment of the specific exploratory perceptual behaviour that would be appropriate for exploring the object imagined if it were actually present. Eye movements are thus a manifestation of such re-enactments that occur during mental-imagery experiences.

Barsalou (1999, 2008) suggests a similar approach where cognition is grounded in the brain’s modality-specific systems and all concepts are represented as perceptual symbols. A perceptual symbol in his sense is not a mental image but a record of the neural activity taking place during perception. Imagery, then, is the re-enactment or simulation of that neural activity. A similar framework has been put forward as part of the simulation theory advocated by Hesslow (2002, 2012). Simulations in his sense include not only sensory states but also motor and mental states. Even so, a simulation is never a complete re-enactment of the original neural activity and may contain distortions. Recalling something that occurred in a specific spatial location will thus make the eyes more likely to revisit that location during the simulation involved.

Enactive theory (Thomas, 1999) and simulation theories of this kind (e.g., Barsalou, 1999; Hesslow, 2012) can very convincingly explain eye-movement effects during imagery, with no need to refer to the format of a possible internal representation. It should be

2.5. THEORIES OF EYE MOVEMENTS DURING MENTAL IMAGERY

noted that these accounts are also largely compatible with the situated framework of spatial indexes (Richardson et al., 2009) mentioned above, meaning that they should not be seen as mutually exclusive, independent explanations. One general difference between them is that spatial indexes are more specifically related to working memory and to executive demands, emphasising the fact that cognition is situated in the external environment, whereas simulation theory, grounded cognition and enactive theory are more general accounts of how information is encoded and retrieved.

Predictions: Simulation theory, grounded cognition and enactive theory predict that eye movements will be executed similarly when a scene is being imagined as when the same scene is being perceived visually. However, according to these theories, the eye movements made during mental imagery are not – as in scanpath theory – an exact replica of the movements made during encoding. The term “re-enactment” used in these accounts refers to the re-enactment of visual perception behaviour in general, not to behaviour during a specific encoding phase. On this view, the oculomotor system cannot distinguish between recollections that are based on a preceding encoding phase and those that are constructed from information retrieved from long-term memory. Those two situations are therefore predicted to generate similar eye movements. On the other hand, owing to individual differences in how the re-enactments are performed, great variability in gaze behaviour is also to be expected. Further, memory retrieval is predicted to be facilitated when there are large overlaps between encoding and recall in the perceptual and sensorimotor processes involved (Kent & Lamberts, 2008).

Chapter 3

Methodology

3.1 Eye-tracking

The recording of eye movements using eye-tracking techniques provides information about the distribution of a person’s visual attention in terms of what objects (e.g. words, pictures or graphics) he or she is looking at, for how long, and in what order. Empirical evidence (as well as common sense) suggests the existence of a link between eye movements and attention shifts (e.g., Schneider & Deubel 1995; Theeuwes et al., 1998; see also Section 2.3 above). It has also been suggested that what is being fixated upon by the eyes indicates what is being processed by the brain. Eye fixations have been seen as representing a “boundary” between perception and cognition, since they are observable indicators of the acquisition of information. Against that background, it has been argued that eye-tracking data can provide an “unobtrusive, sensitive, real-time behavioral index of ongoing visual and cognitive processing” (Henderson & Ferreira, 2004, p. 18).

When we act upon the world and look at things, our eyes do not move in a smooth, uninterrupted fashion. The process as observed has been broken down into a number of different “events”. One of the most common ones is the fixation. A fixation is when the eyes remain relatively still over a period of time, for instance when they stop at an object shown in a picture or at a word during reading. Typically lasting for around 200–300 ms, its duration can range from tens of milliseconds to several seconds. It is widely assumed that the duration of a fixation is an indication of the amount of cognitive processing taking place (Rayner, 1998). A second frequent event is the rapid movement from one fixation point to another, which is called a saccade. Saccades are the fastest movements the body can produce and are typically completed within 30–80 ms. Virtually no visual information at all is obtained during a saccade (Rayner, 1998). A third type of event is a slower type of movement called smooth pursuit, which we make when our eyes are following a moving object, such as a car driving on a road. In principle, smooth pursuit can occur only in situations where we are following a moving object, whereas saccades can be executed without any specific external cues (but see Lorenceau, 2012, for evidence of volitional control over smooth pursuit).

Fixations, saccades and smooth pursuit are the three major eye-movement events. There are also several types of micro-movements whose purpose is mainly compensatory and/or stabilising, even though there is evidence that some of them are also related to cognitive processing. For instance, during a fixation there occur small movements called micro-saccades, which have been found to frequently indicate the direction of covert attention shifts (e.g., Rolfs, 2009).

In the studies presented in this thesis, however, the only eye-movement events investigated are fixations and saccades. For a detailed overview of all eye-movement events and their roles in visual cognition, see Holmqvist et al. (2011).

3.1.1 Eye-tracking, cognition and mental imagery

Eye-tracking has been found to provide invaluable insights into visual cognition in a wide range of disciplines and research fields (see Holmqvist et al., 2011). In cognitive psychology, most eye-tracking studies have focused on reading, scene perception and visual search. When we are reading, our eyes move in a rather systematic pattern from word to word, which makes eye-tracking an ideal method to study this behaviour. Typical experiments in reading research focus on single sentences and investigate how lexical and syntactic factors influence reading behaviour. Eye-tracking in reading research has a long tradition and has revealed a great deal about how texts are processed (for an overview, see Rayner, 1998).

The focus of scene-perception research is on how we look at visual scenes, and eye-tracking is a natural method to investigate this issue as well. However, the eye movements observed during scene perception are less systematic than those seen during reading and are also influenced by many factors. Typical experiments investigate either the influence of “bottom-up” factors linked to the scene itself or the influence of “top-down” factors related to the viewer, such as the effect of having different goals. There is evidence that bottom-up factors such as contrast, colours and luminance determine where our attention and our eye movements are guided during scene perception (e.g., Itti, 2006). Based on such low-level features, a “saliency map” of a scene can be computed and used to predict where in that scene people will look (e.g., Itti & Koch, 2001). Still, even if bottom-up factors linked to the scene itself influence where we will look to a certain extent, they are often overridden by top-down factors, such as schema knowledge about how to look at a certain type of image, expertise in various fields, cultural differences and personal preferences (e.g., Underwood et al., 2006; Henderson & Ferreira, 2004). For instance, Yarbus (1967) demonstrated in his seminal work that the task instruction given exerted a very strong influence on how participants looked at a painting.

Research on visual search is a specific type of perception research and has a strong eye-tracking tradition, too. The basic idea of these studies is for participants to search visually for an object until they find it or decide that it is absent. Typical experiments include a set of items consisting of targets and distractors, with properties (e.g. size, amount, colour) that can be varied between experiments. Eye-tracking studies of visual search have revealed a great deal about visual cognition and about the limitations and affordances of our visual system (e.g., Hooze & Erkelens, 1996; Wolfe, 1998).

In the studies presented in this thesis, eye-tracking is used in a slightly atypical way, namely to investigate participants’ eye movements when they are looking “at nothing”. Since the participants have nothing to look at, there are no relevant bottom-up features to guide their visual attention. Therefore the mental-imagery tasks performed by them represent the most extreme case of top-down processing.

A crucial question whenever eye-tracking is used in research on mental imagery is the relationship between overt attention (for which the direction of the gaze is used as a proxy) and covert attention. As mentioned above, there are situations where eye movements can be decoupled from attention (e.g., Posner, 1980). Therefore, shifts of attention during mental-imagery tasks could potentially be executed covertly without overt eye movements. Then eye-tracking would not reveal anything useful at all. However, there is an ample

3.1. EYE-TRACKING

amount of eye-tracking research suggesting that covert attention shifts are soon followed by overt saccades with the purpose of guiding the eyes to a specific new region of interest (e.g., Deubel & Schneider, 1996). Moreover, it has been suggested that covert attention is actually the same as the programming of a saccade (e.g., Deubel & Schneider, 1996; Irwin & Gordon, 1998; Theeuwes, Olivers & Chizk, 2005). In support of this view, it has been shown that the activity observed in the visual cortex is similar whether saccades to remembered locations are performed (corresponding to an overt attention shift) or only programmed but never actually executed (corresponding to a covert one) (Geng, Ruff, & Driver, 2009). Against the background of this research and previous studies of eye movements during mental imagery (e.g., Brandt & Stark, 1997; Laeng & Teodorescu, 2002), eye-tracking seems able not only to measure what we are looking at in the outside world, but also how we are looking at imagined scenes “with the mind’s eye”.

3.1.2 Video-based eye-tracking

The majority of eye-trackers use a video-based system to measure eye movements (see Holmqvist et al., 2011). The method used in these systems to determine where someone is looking is to film the eye while illuminating it with a beam of infrared light. This technique makes it possible to identify both the pupil and the corneal reflection of the light beam in the video. The corneal reflection serves as a second reference point in this set-up, and it is needed to compensate for small head movements (Holmqvist et al., 2011). Figure 6 shows an eye image where both the pupil and the corneal reflection have been identified.

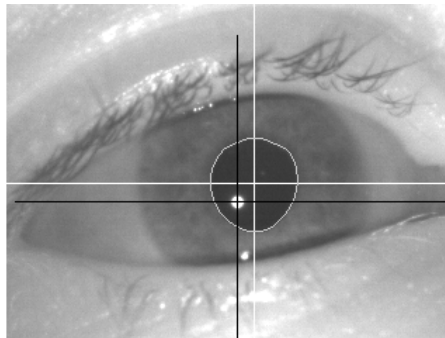


Figure 6: A video-based system which has identified the pupil (white crosshairs) and the corneal reflection of the infrared-light beam (black crosshairs) in the image of the eye.

Video-based eye-trackers can be either static or head-mounted. Static eye-trackers film and illuminate participants’ eyes from a fixed position, whereas head-mounted eye-trackers film and illuminate participants’ eyes from equipment mounted on their head (for a detailed overview, see Holmqvist et al., 2011). In the investigations presented in this thesis, both a head-mounted and a static eye-tracker were used.

In Paper I, the SMI iView X HED + HT, recording data at 50 Hz, was used. This eye-tracker consists of a bicycle helmet with a scene camera and an eye camera (Figure 7 shows a participant wearing this head-mounted system). The system also includes magnetic head-tracking, which allows large body and head movements. This particular system was chosen over others because participants would be looking at stimuli larger than a computer screen. Static eye-trackers can typically track the eyes only within the limited space provided by a computer display. Further, in two of the experiments in Paper I, participants were “looking” at an entire wall in complete darkness. To my knowledge, there is no static eye-tracker capable of handling such a situation.



Figure 7: Example of the head-mounted eye-tracker used in Paper I. The device generating the magnetic field is located in the upper part of the figure.

In Papers II and III, the SMI iView RED 250, recording data at 250 Hz, was used, and in Paper IV, the SMI iView RED 500, recording data at 500 Hz, was used. Both systems are “remote” eye-trackers, a specific type of static eye-tracker which films the eyes from below the computer display (Figure 8 shows this system with the camera below the monitor) and allows participants to move their body and head to some extent without causing data to be lost. Those particular systems were chosen because certain conditions in these studies included an eye-movement restriction which depended on a computer-based manipulation. What is more, those systems allow participants to sit naturally at the computer without wearing or seeing any additional equipment, which often makes them forget that the eye-tracker is there. This is valuable, since the participants had to be naive to the fact that their eyes were being tracked in all of these studies.



Figure 8: Example of a remote eye-tracker (the arrow shows where the camera is located) as used in Papers II, III and IV.

3.2 Analysing eye movements during mental imagery

To compare the scanpaths from the recall phase involving mental imagery with those from the encoding phase involving visual perception, Brandt and Stark (1997) used a string-edit measure (Levenshtein, 1966) to assess similarity in terms of spatial structure and sequential order. The basic idea of the string-edit method is first to convert a sequence of fixations into a string of characters by breaking down the stimulus into labelled regions. The similarity between the string from the encoding phase and that from the recall phase is then computed by calculating the minimum number of editing operations (insertions, deletions and substitutions) required to turn one string into the other. For further details, see Holmqvist et al. (2011, pp. 268–271).

Several recent studies based on scanpath theory and using the string-edit measure have been carried out to investigate eye movements during mental imagery in this manner (Gbadamosi & Zangemeister, 2001; Humphrey & Underwood, 2008; Laeng & Teodorescu, 2002; Liman & Zangemeister, 2012; Zangemeister & Liman, 2007).

However, one considerable problem with this method is that it is based on the assumption that there is a one-to-one relationship between spatial co-ordinates from encoding and recall. For example, if a participant looked at a certain object shown in a certain location on the screen during encoding, the co-ordinates of that location are deemed to correspond to that object when the screen is blank during recall. This assumption does not consider individual differences between people as regards their eye movements. One relevant such difference reported by previous studies is that the scanpaths observed during recall frequently occupy a smaller area than those observed during encoding even though they retain the same overall shape (Brandt & Stark, 1997; Gbadamosi & Zangemeister, 2001).

Other studies have used an even simpler analysis, only considering gaze positions in specific segments of the computer screen (Richardson & Spivey, 2000; Spivey & Geng, 2001; Altmann, 2004). A similar approach was used in Paper IV in this thesis, where the consequences of looking at blank spaces during memory retrieval were targeted.

3.2.1 Correspondence between eye-movement and verbal data

As has been described above, there are certain limitations to a method focusing on how the position of the eyes during a recall phase involving mental imagery corresponds to the position of the eyes during a preceding encoding phase involving visual perception. Eye movements are idiosyncratic and gaze patterns are frequently compressed to a smaller area during mental imagery. One way round this problem is to investigate only the direction of eye movements, not their distance. Spivey and Geng (2001, Experiment 1) used such a directional approach, measuring eye movements in relation to four directions: left, right, up and down. However, to obtain more detailed information about what is happening than mere directions, there is a need to link the spatial layout of the eye-movement data to the time dimension. Apart from the study by Altmann (2004), this dimension has either largely been ignored or has – with the string-edit technique – been reduced to the sequential order of the components of a scanpath (Brand & Stark, 1997; Gbadamosi & Zangemeister, 2001; Humphrey & Underwood, 2008).

Eye-movement records naturally comprise both spatial and temporal information, meaning that they have the potential to show where on a stimulus a cognitive process operated, when it occurred and how long it lasted. In experiments with carefully designed

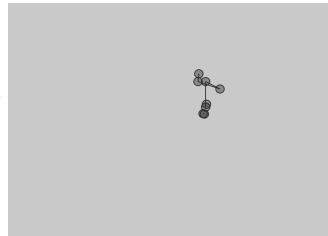
stimuli and well-defined tasks (e.g. in visual search), eye-tracking data can thus reveal much about the identity of the processes involved. However, in mental-imagery experiments, where participants are basically looking at nothing, it is very difficult to establish temporal links between gaze patterns and specific cognitive processes using eye-tracking data alone. One solution to this problem is to combine eye-tracking data with verbal data, which can be recorded concurrently with eye-tracking data and which have a strong disambiguating potential (e.g., Holsanova, 2001, 2008; Van Gog, Paas, & Van Merriënboer, 2005).

An experimental paradigm combining eye-movement data with verbal data during mental imagery was introduced in the study by Holsanova et al. (1999), where it was observed that participants who orally described a complex picture from memory made eye movements that reflected, in line with the temporal progression of their descriptions, the spatial structure of the picture described. Access to eye-movement data recorded concurrently with a verbal description can thus be assumed to make it possible to determine what part of a mental image a participant was attending to at a certain time, meaning that the eye-movement data can be analysed against that background.

This combination of verbal reports and eye-movement data during mental imagery is further developed in Paper I and Paper III in this thesis, where it is used as a novel method to investigate in detail how eye movements relate to visualised properties over time. Figure 9 below shows an example of eye movements and statements made concurrently by a participant looking at a blank screen while describing the scene represented in Figure 10.

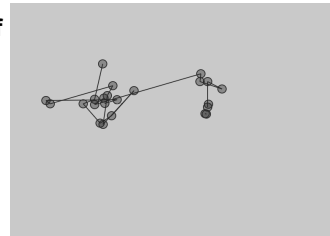
(A) - 0 to 10 sec.

"Well, in the middle of the picture there is a large spruce ... there is a bird at the top of it"



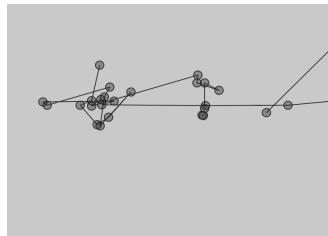
(B) - 10 to 26 sec.

"And in the left of the picture there is a yellow house with a bird at the top of it I think it was"



(C) - 26 to 40 sec.

"And ehm in the right of the picture there is a tree which has red and yellow leaves"



(D) - 40 to 57 sec.

"And to the left of it there is a man wearing a boiler suit. And in front of this stuff there is a red fence"

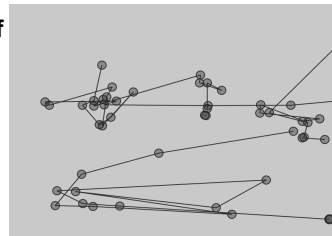


Figure 9: Example of a participant's (additive) gaze pattern while she is retelling the scene illustrated in Figure 10 during four time intervals. To the left of each gaze pattern is a transcription of the verbal data produced concurrently with the new part of the gaze pattern (here translated into English).

3.2. ANALYSING EYE MOVEMENTS DURING MENTAL IMAGERY

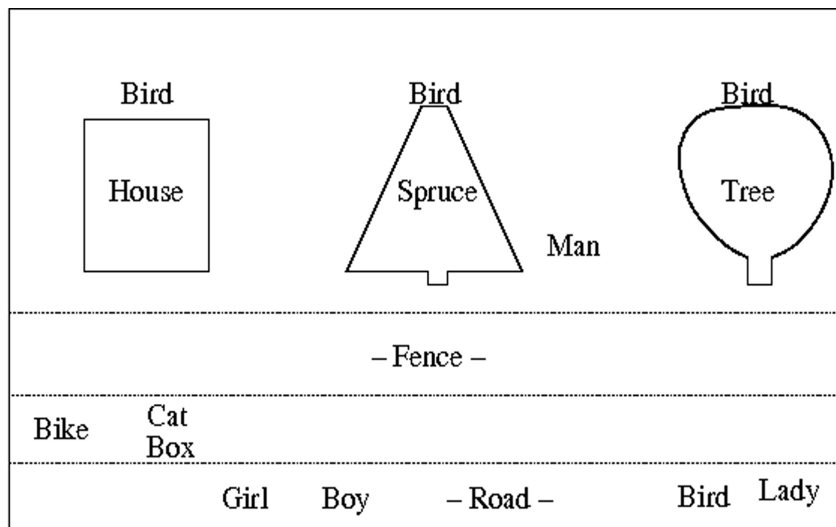


Figure 10: Spatial schematics for the objects included in the pre-recorded description used as verbal stimulus in Papers I and II.

3.2.2 Spatial dispersion of gaze patterns

In Papers II and III, the overall spread of eye movements during encoding and recall was a crucial aspect to be investigated. Therefore it was necessary to find an appropriate measure for the spatial dispersion of participants' gaze patterns. A modified version of the coverage measure proposed by Wooding (2002), as described in Holmqvist et al. (2011, p. 367), was chosen for this purpose. This measure relates to the extent to which the computer screen was covered by the fixations. It was chosen over other coverage measures because the impact of a single fixation is very small (i.e. it is relatively "outlier-proof"). Other, more established coverage measures, such as the convex-hull area (Goldberg & Kotval, 1999), weight all fixations equally and would therefore not be suited for these investigations. In relation to the spatial spread of eye movements, Wooding's measure is conservative, and infrequent fixations far away from the main cluster do not disproportionately influence the overall calculation of spatial dispersion. For example, if a participant was mostly looking at the centre of the display for an entire session but made occasional saccades to the edges of the display, those saccades will not have any significant effect on the overall measure of spatial dispersion (see Figure 11b). By contrast, such outliers would have enlarged the convex-hull area for that participant in a way that would seem disproportionate.

The mathematics behind this measure are described in detail in Holmqvist et al. (2011, p. 367). The basic idea is as follows: An "attention map" is created by centring a three-dimensional Gaussian function at each fixation point (the standard deviation σ was set to span 10% of the screen width, i.e. $\sigma = 0.1 \times 1680$ pixels). Next, all the Gaussian functions are superimposed upon each other. The volume under the attention map, after being normalised to unit height, is used as a measure of the spatial dispersion of the gaze pattern. Wooding (2002) uses a landscape metaphor to describe this procedure, likening the highest – most relevant – "peaks" in the attention map to islands in a sea (see Figure 11 for examples of such "terrain visualisations"). Finally, the computed volume is normalised against its maximum theoretical value ($1680 \times 1050 \times 1$), which yields a value between 0 and 1. This value will be closer to 1 if the fixations are evenly distributed across the entire computer screen than if there are densely packed pockets of fixations. See Figure 11 for examples of high and low spatial-dispersion values.

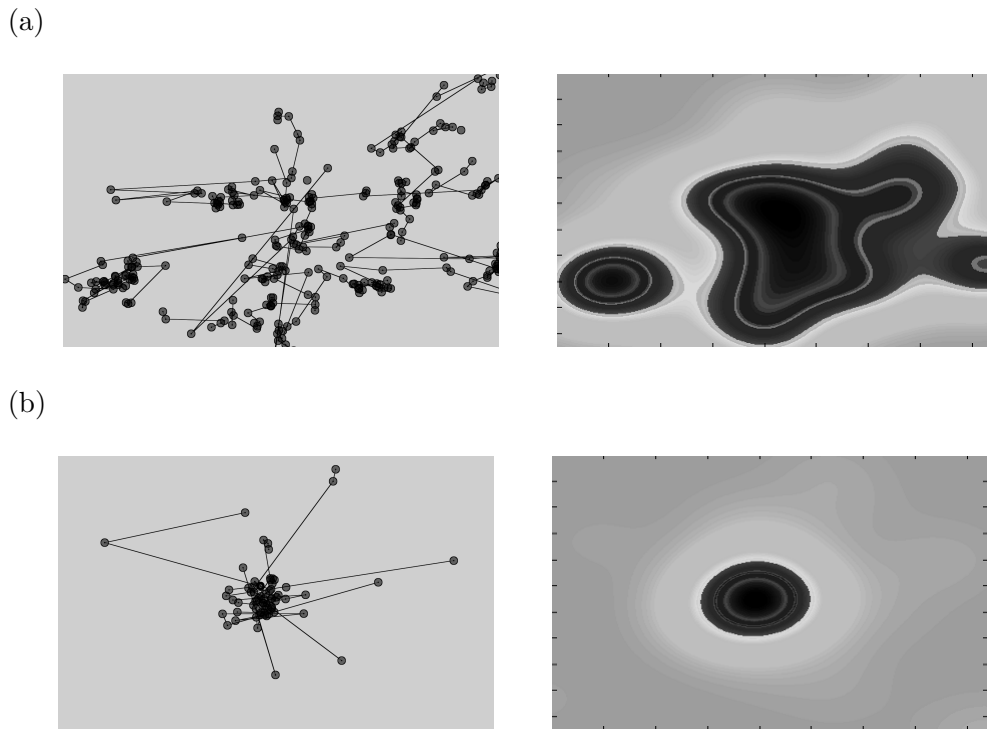


Figure 11: Example of two participants’ gaze patterns (left) and the corresponding “terrain visualisations” after Wooding’s (2002) coverage measure has been applied (right). Using Wooding’s landscape metaphor, coverage in this visualisation is represented as islands rising above the water. The top pair (a) represents a participant with a high coverage value of 0.41 and the bottom pair (b) represents a participant with a low coverage value of 0.09.

3.2.3 Eye movements as independent variables

In Papers III and IV, eye movements were manipulated as independent variables in order to assess the impact of how and where participants look during mental imagery and episodic-memory retrieval. Specifically, participants were told how and where to look during encoding and recall. In the conditions with imposed gaze behaviour, the eye-tracking data were used to exclude from further analysis any sessions where a participant failed to comply with the instructions. For example, in Papers III and IV one of the imposed eye-movement restrictions was for participants to maintain fixation on a fixation cross at the centre of the screen. Sessions where a participant made one or more fixations at positions more than 3 degrees away from the centre of the fixation cross were excluded (see Figure 12).

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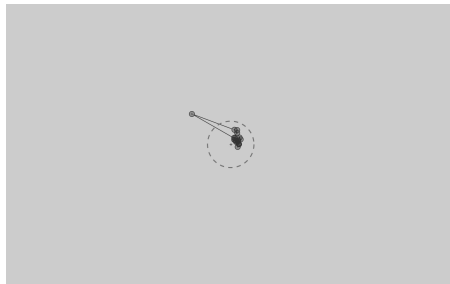


Figure 12: Gaze pattern of one participant during a session for Paper IV. The imposed gaze restriction in the experiment in question was for the participant to fixate on a fixation cross at the centre of the screen. The dashed circle represents the 3-degree exclusion threshold (which was not visually present during the actual session). This participant did not stay within that circle during the session, and the data from that session were therefore excluded from further analysis.

Chapter 4

The investigations

4.1 Paper I: Eye movements during mental imagery

Paper I used a novel experimental method where eye movements during mental imagery were investigated over time in relation to verbal protocols in a series of four experiments.

4.1.1 Verbal versus visual elicitation

In Experiment 1, eye movements during mental imagery were investigated for a verbally described scene. Participants first listened to a spoken scene description while looking at a blank screen. In the subsequent recall phase, they retold the scene from memory while looking at the same blank screen. Eye movements were monitored both while the participants were listening to the scene description and while they were retelling it. The goal of Experiment 1 was twofold. First, previous investigations of verbal descriptions and eye movements to blank spaces had only considered simple directions (Demarais & Cohen, 1998; Spivey et al., 2000; Spivey & Geng, 2001). We focused on complex spatial relationships (e.g. “at the centre”, “between”, “above”, “to the far right”, “to the left of”, “on top of”) and carried out a detailed investigation of how eye movements corresponded to this information in a coherent scene description. Second, besides investigating eye movements while participants were listening to a spoken scene description, we added a recall phase in which they retold the scene described from memory, so that we would be able to compare eye movements during encoding with those during recall.

In Experiment 2, eye movements were investigated during participants’ recollection of a complex picture. Participants first visually inspected a complex picture. In the subsequent recall phase, they orally described that picture from memory while looking at a blank screen. Eye movements were monitored both while the participants were inspecting the picture and while they were describing it from memory. The goal of Experiment 2 was also twofold. First, by using as our stimulus a naturalistic picture rich in detail and of high complexity, we wanted to go beyond previous studies, which had used relatively simple stimuli. For example, Brandt and Stark (1997) used a six-by-six black-and-white grid pattern during their encoding phase, and Spivey and Geng (2001) used four different shapes in the corners of a three-by-three grid. In fact, findings from other types of mental-imagery studies indicate that the ability to visualise a scene is highly dependent on its complexity (e.g., Kosslyn, 1994, Chapter 9). Second, by comparing the results from this experiment with those from Experiment 1, we were able to investigate whether the effect

of eye movements to blank spaces during mental imagery was equally strong irrespective of whether the original stimulus had been spoken or visual. This comparison has important theoretical implications with regard to the functional role of eye movements and of the visual system during mental imagery.

4.1.2 Light versus complete darkness

In Experiments 3 and 4, Experiments 1 and 2 were replicated with a single difference: they were conducted in complete darkness (except the visual inspection of the picture in Experiment 4, where a small pilot study had revealed that nobody could see the picture until we switched the light on). Thus, instead of looking at a blank screen while listening to the scene description, while retelling it and while describing the picture from memory, participants did this in complete darkness. The goal of Experiments 3 and 4 was to investigate whether eye movements during mental imagery are used to bind imagined elements to external visual cues in the environment, as proposed in Pylyshyn's (2002, p. 181) visual-index theory, or whether they are linked to the internal processes giving rise to mental-imagery experiences. If eye movements are shown to reflect content and spatial relationships when participants are engaged in a mental-imagery task carried out in complete darkness, then a theory which explains the occurrence of eye movements during mental imagery solely with reference to an association between eye movements and visual features in the outside world will be invalid.

4.1.3 Results

The results from Experiment 1 extended the findings by Demarais and Cohen (1998), Spivey et al. (2000) and Spivey and Geng (2001) by showing that participants who listened to a spoken scene description while looking at a blank screen spontaneously performed eye movements that closely corresponded to spatial positions and directions inherent in the description they were listening to. We also found a similar effect when the participants themselves were retelling the scene from memory.

The results from Experiment 2 were similar to those obtained in previous studies using simple artificial stimuli during encoding (Brandt & Stark, 1997; Spivey & Geng, 2001; Laeng & Teodorescu, 2002). It extended those studies by showing that eye movements to blank spaces during mental imagery occur during the recollection of complex naturalistic pictures as well.

Comparison of the results from Experiments 1 and 2 revealed that the eye-movement effect was equally strong irrespective of whether the original stimulus was spoken or visual. Further, by using our combination of eye-tracking and verbal reports, we were also able to investigate the eye-movement effect in much greater detail than previous studies had been able to do.

The results from Experiments 3 and 4 demonstrated that the eye-movement effect occurred even in complete darkness. This finding has crucial theoretical implications in that it falsifies Pylyshyn's (2002, p. 181) visual-index explanation for eye movements during mental imagery.

4.1.4 Open questions

In Paper I, we also found that participants frequently appeared to “shrink” their mental images: while visualising the picture they had previously seen, they looked only at a part

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of the screen which was smaller than the area that the picture had occupied. Within this smaller area, however, positions and directions from the picture visualised were preserved in their eye movements. The same tendency was found for those who listened to the verbal scene description. Some of them “painted” the scene with their eyes over the entire blank screen while listening, whereas others looked only at a limited part of the screen, and this gaze behaviour was largely preserved during recall: those who had looked at a smaller area while listening to the scene description looked at a similar area while retelling it, and those who had looked at the entire board behaved in a similar way while retelling. There was also one participant (out of twelve) who maintained his gaze at the centre of the blank board while recalling the picture and did not make any corresponding eye movements at all, as well as two participants (out of twelve) who exhibited no “eye-movement effect” either while listening to the scene description or while retelling it in the subsequent recall phase.

Gaze patterns differing in size between encoding and recall have also been reported by Brandt and Stark (1997) and by Gbadamosi and Zangemeister (2001). What is more, two of the nine participants in the study by Brandt and Stark (1997) did not exhibit any eye movements during visual imagery, and nor did two of the twelve participants in the study carried out by Spivey et al. (2000).

These large individual differences in gaze patterns during recall do bring into question the actual strength of the relationship between eye movements during recall and eye movements during encoding.

Furthermore, while the phenomenon of looking at empty spaces during mental imagery was thoroughly investigated in Paper I, the role of such eye movements, in respect to image formation, image inspection and memory retrieval, was not investigated at all.

4.2 Paper II: Individual differences in gaze patterns

In Paper II, the open question from Paper I concerning individual differences in gaze patterns during mental imagery was investigated. Specifically, we focused on the finding that some participants' gaze patterns are “scaled down” during scene recollection to an area smaller than that occupied by the stimulus encoded.

There have been few previous studies dealing with eye movements and individual differences during mental imagery. However, an early study by Marks (1973a) reported that participants who experienced very poor visualisations during pictorial recall had a higher eye-movement rate (EMR) than those who experienced very vivid visualisations. Further, studies of working-memory capacity have found a strong relationship between the ability to control eye movements and working-memory capacity (e.g., Kane, et al., 2001). Based on these studies, we hypothesised that individual differences in eye movements to blank spaces during mental imagery might be associated with different levels of mental-imagery ability and/or working-memory capacity.

The experiment reported in Paper II was therefore designed to explore whether individual differences in object-imagery ability, spatial-imagery ability and working-memory capacity are related to how eye movements spread out and correspond to content and spatial layout during mental imagery. As mentioned above, object imagery refers to the processing of information about appearance, colour, shape and texture (the “what” aspect) and spatial imagery refers to the processing of information about location, spatial relationships, movement and transformation (the “where” aspect).

The experiment was divided into three parts. In the first part, participants first inspected a complex picture and then orally described that picture from memory while looking at a blank screen. In the second part, they were tested for working-memory capacity in an operation-span task (Unsworth, Heitz, Schrock & Engle, 2005). In the third and final part, they answered the Object–Spatial Imagery and Verbal Questionnaire (OSIVQ) (Blazhenkova & Kozhevnikov, 2009), which assesses both object-imagery and spatial-imagery ability.

4.2.1 Results

The results replicated the findings from Paper I, showing that the participants' eye movements while they were looking at a blank screen during pictorial recall closely reflected both content and spatial layout. The results also revealed that the gaze patterns of participants with poor spatial-imagery ability were closer to the original size of the picture encoded than the gaze patterns of those with stronger spatial-imagery ability. However, no relationship was found to working-memory capacity.

4.2.2 Open questions

In Paper II, we found evidence that gaze patterns during scene recollection are related to individual differences in visuospatial-imagery capabilities. However, that finding was based only on a correlative relationship between eye movements and scores on the OSIVQ. We were therefore not able to make any causal claims about how eye movements are related to visuospatial processing and different memory representations.

4.3 Paper III: The role of eye movements

In Paper III, the open question from Paper I concerning why eye movements “to nothing” occur during mental-imagery tasks was investigated. To fully understand the role of eye movements during mental imagery, two fundamental questions must be answered.

The first question is to what extent the oculomotor system is involved in mental imagery and memory retrieval. There is an accumulating body of research suggesting that when we are engaged in mental imagery and tasks of memory retrieval, a cognitive system at least partly reactivates processes that were involved in the preceding encoding phase (for an overview, see Kent & Lamberts, 2008), but there is not much evidence as regards the extent of the involvement of the oculomotor system. The second question is whether eye movements to blank spaces can facilitate memory retrieval. On this point, the results reported in the literature are mixed. More specifically, there are results suggesting that eye movements during recall are functionally connected to those produced during encoding (Brandt & Stark, 1997; Laeng & Teodorescu, 2002) and that they facilitate memory retrieval (Janssen & Nodine, 1974; Laeng & Teodorescu, 2002), but there are also results indicating that eye movements during recall are only epiphenomenal in relation to those produced during encoding (Richardson & Spivey, 2000, Experiment 5) and therefore do not assist memory-retrieval processes in any useful way (Hoover & Richardson, 2008; Richardson & Kirkham, 2004; Richardson & Spivey, 2000; Spivey & Geng, 2001).

Experiments 1 and 2 of Paper III were designed to test whether eye movements during recall are functionally connected to those made during encoding. To obtain a reliable answer to the question of whether oculomotor events or processes from encoding are reactivated during recall, we used complex stimuli and demanding recall tasks, which drew heavily on visuospatial information from the encoding phase, and we introduced a central-fixation restriction during the encoding phase. Our use of both complex pictures and a spoken scene description as stimuli (as in Paper I) also enabled us to investigate whether the effect of this restriction differed between visually encoded scenes (Experiment 1) and abstract scenes with comparable semantic and spatial characteristics encoded without visual input (Experiment 2).

Experiments 3 and 4 of Paper III were designed to test whether eye movements “to nothing” have an active role with respect to how the original scene is recalled and remembered. The method used for doing this was to allow the participants to look freely during the encoding of an original picture (Experiment 3) or during the encoding of a verbal scene description (Experiment 4) and then prohibit eye movements during recall by introducing a central-fixation restriction.

4.3.1 Results

Experiment 1 showed that even though the participants had maintained central fixation during the encoding of a complex picture, during recall their eye movements spread out and corresponded to positions and directions of the original picture. Experiment 2 similarly showed that maintaining central fixation during the encoding of a spoken scene description did not affect the spread of eye movements or their correspondence to positions and directions of the scene during recall. These results contradict the hypothesis (see Laeng & Teodorescu, 2002) that eye movements during scene recollection replicate those made during encoding. Instead, it must be concluded that eye movements during mental imagery largely operate independently of those made during encoding.

Experiment 3 showed that maintaining central fixation during pictorial recall affected how the original picture was recalled (the picture descriptions focused significantly more

on general aspects of the picture than on objects, details and events, and significantly fewer objects were reported, compared with the condition where recall was performed without eye-movement restrictions). Finally, Experiment 4 showed that maintaining central fixation during recall of a scene description impaired memory of the scene during recall (significantly fewer objects and object locations were remembered in the retellings of the scene). This finding indicates that eye movements during scene recollection are not a mere epiphenomenon but can indeed play an active and supportive role during memory retrieval.

4.3.2 Open questions

In Paper III, we found evidence that eye movements played a functional role during scene recollections performed in Experiments 3 and 4. However, the participants were not actually asked to try to remember as much as possible in those experiments. Therefore it is difficult to make any strong claims with respect to memory retrieval as such and with respect to whether eye movements “to nothing” can act as facilitatory retrieval cues. In addition, the reason, or part of the reason, for the impaired recollection performance could in fact be the cognitive cost of performing the additional task of maintaining central fixation: the task of concentrating on the fixation cross may have tapped into general cognitive resources to such an extent that the participants were impaired in their ability to describe the picture. This is an alternative explanation of the results which Paper III could not rule out.

4.4 Paper IV: Relationship to memory retrieval

In Paper IV, the open question from Paper III concerning the relationship between looking “at nothing” and retrieval performance was thoroughly investigated.

A single experiment was conducted where this question was addressed by means of direct eye-movement manipulation in the retrieval phase of an episodic-memory task. Four conditions were used: (1) free viewing on a blank screen, (2) maintaining central fixation, (3) viewing within a square congruent with the location of the objects to be recalled, and (4) viewing within a square incongruent with the location of the objects to be recalled.

The results from Papers II and III had suggested that the principal benefit of looking “at nothing” is not that it helps to process information related to appearance but that it assists in visualising locations and spatial relationships. There is a great deal of evidence suggesting that different parts of the brain, namely the ventral (“what”) and dorsal (“how/where”) streams of visual processing (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982), are fundamental to object and location memory, respectively (e.g., Farah et al., 1988; Pollatsek, Rayner, & Henderson, 1990). It is therefore conceivable that the influence of gaze behaviour on visuospatial remembering may be different for intrinsic features of objects than for the spatial relationship(s) between two or more objects. Paper IV made it possible to compare memory for intrinsic object features with memory for spatial relationships between objects (“intra-item” versus “inter-item” memory).

Additionally, in contrast to previous work (for an overview, see Ferreira et al., 2008; Richardson et al., 2009), the analyses of memory performance included response times (RT). This complements binary measures of accuracy, providing a potentially more sensitive measure of the availability of the memory trace to be recalled (Sternberg, 1969).

4.4.1 Results

First, results from the blank-screen condition replicated previous findings that eye movements are spontaneously executed towards empty locations where information was previously encoded (Richardson & Spivey, 2000; Spivey & Geng, 2001). What is more, the total scanpath was significantly longer during inter-object trials than during intra-object trials, which indicates that the retrieval of spatial relationships between two objects elicits a longer overall scanpath than the retrieval of visual properties of a single object. This adds support to the claim that eye movements during visuospatial recollection mirror content and spatial relationships.

Second, it was shown that the very act of moving the eyes can influence visuospatial remembering. A central-fixation constraint impaired retrieval performance (as indicated by longer RTs) for inter-object memory. This finding adds weight to the results from Paper III, and it further suggests that memory for spatial relationships between objects is more readily affected than memory for intrinsic object features.

Third, the results confirmed that memory retrieval is indeed facilitated when the position of the gaze is manipulated towards a blank area that corresponds to the original location of the object recalled. The results were robust with respect to both memory accuracy and RTs, and they were clear irrespective of memory type. Gaze behaviour manifesting compatibility between the encoding and retrieval conditions thus increases the likelihood of successful episodic remembering.

Finally, the comparison between the congruent-square condition and the incongruent-square condition addressed the potential confounding factor of differences in cognitive load that could not be excluded in Paper III, as the additional task (keeping one’s gaze within an empty square) was identical in both conditions.

Compliance with the eye-movement restrictions imposed

Because of limitations to the space available, analyses of data from the excluded sessions – i.e. the ones where participants failed to comply with the eye-movement restrictions imposed on them – were not included in Paper IV. Since those sessions may provide valuable information about the causal relationship between eye movements and memory retrieval, they are further investigated in this section instead.

Table 1 presents average numbers of excluded sessions in the three conditions with eye-movement restrictions: central fixation, congruent square and incongruent square.

Table 1: Average number of excluded sessions per participant in the experiment reported in Paper IV, broken down by eye-movement condition and memory-type condition, with standard deviations in parentheses. For each of the 24 participants, there were a total of 48 sessions with each eye-movement condition (24 intra-object and 24 inter-object ones).

	Central fixation	Congruent square	Incongruent square
Intra-object	2.5(2.6)	0.7(1.0)	2.0(2.2)
Inter-object	4.0(3.5)	2.0(2.0)	3.1(3.0)

A Wilcoxon signed-rank test showed that there were significantly more excluded inter-object sessions than intra-object sessions ($Z = -2.549$, $p < .01$), and a Friedman test showed that there was a significant difference in the number of excluded sessions across eye-movement conditions ($\chi^2(2) = 11.318$, $p < .01$). Post-hoc analysis with Wilcoxon signed-rank tests revealed that significantly fewer sessions were excluded in the congruent-square condition than either the incongruent-square condition ($Z = -2.949$, $p < .01$) or the central-fixation condition ($Z = -3.436$, $p < .01$). No significant difference in the number of excluded sessions was found between the central-fixation and incongruent-square conditions.

Finally, the eye movements from excluded sessions were explored with regard to the quadrant of the screen to which the saccades were executed. In the central-fixation condition, 66% (intra-object: 72%, inter-object: 63%) of all excluded sessions had saccades to the “critical” quadrant (the one in which an object being recalled had been located in the encoding phase). In the incongruent-square condition, 29% (intra-object: 27%, inter-object: 30%) of all excluded sessions had saccades to the critical quadrant. At first glance, this result would appear to indicate that the participants were not particularly prone to execute saccades to the critical quadrant during the incongruent-square condition. However, the experimental design of this condition was such that saccades rarely landed outside the quadrant in which the incongruent square was located (60% of saccades in excluded intra-object sessions and 56% of saccades in excluded inter-object sessions remained within the same quadrant as the incongruent square). By contrast, and by definition, all quadrants were within easy reach of the central point of the screen.

To sum up, participants found it more difficult to comply with the eye-movement restrictions imposed on them in the central-fixation and incongruent-square conditions than in the congruent-square condition, and more difficult to do so during inter-object statements than during intra-object statements. Further, a large proportion of the “illegal” eye movements were executed to the critical quadrant.

This adds further support to the claims that eye movements are functionally connected to the retrieval of visuospatial memories and that memory for spatial relationships is more readily affected by manipulation of eye-movement behaviour than memory for intrinsic object features.

Chapter 5

Conclusions

It does not seem plain, at first, that the retention of an idea, an image, in the mind is the work of our voluntary muscles. What are the movements produced, when I conceive to myself a circle, or think of St. Paul's? We can answer this question only by supposing that the mental image occupies in the brain and the other parts of the nervous system the same place as the original sensation. As there is a muscular element in our sensations, particularly in those of the highest order - in touch, sight, and hearing - this element must, in some way or other, find its place in ideal sensation - recollection.

Alexander Bain (1855)

5.1 Principles of eye movements during mental imagery

To conclude, I will describe the characteristics of the major discoveries stemming from the studies included in this thesis in terms of four unifying principles of eye movements during mental imagery. Then I will evaluate current theories that attempt to explain eye movements during mental imagery (as described in Section 2.5) against the background of those principles. In this context, I would like to stress once again that it is important to keep in mind that these theories have not been developed as alternatives to each other and that they should not be seen as mutually exclusive competitors. Finally, I will relate the findings to more general theories within contemporary cognitive science.

The first principle that I have identified, which was supported by all four papers included in this thesis, is that *spontaneous eye movements “to nothing” occur during mental imagery, and such eye movements correspond to spatial relationships and content of the scene being visualised.* Paper I specified this principle further by showing that it does not matter whether the scene recalled originates from a previous encoding phase or whether it is constructed directly from long-term memory. Paper II demonstrated that this principle is dependent upon individual differences in visuospatial capabilities and that there is a great deal of variability among individuals in how these eye movements are executed. For instance, participants often kept their gaze within an overall area which was smaller than the space that the scene being recalled had originally occupied.

The second principle identified is that eye movements “to nothing” during mental imagery are *dependent upon spatial relationships and content of the scene being visualised*. In other words, such eye movements are not simply an effect of associating imagined objects with locations in the external environment. This was shown in Experiments 3 and 4 of Paper I, where it was found that eye movements during mental imagery occur even in complete darkness. However, it has also been demonstrated and discussed in this thesis that the eye-movement effect can be stronger or weaker depending on the support available from information in the outside world.

The third principle identified is that eye movements “to nothing” during mental imagery *do not constitute a reproduction of the oculomotor activity produced during perceptual encoding*. In other words, the eye-movement effect does not simply represent the outward manifestation of a procedural motor memory of how the eye movements were executed during the preceding encoding phase. This was shown in Experiments 1 and 2 of Paper III, where it was demonstrated that eye movements were executed to blank spaces that corresponded to a mental image of the scene being recalled even if participants’ gaze had been maintained on a fixation cross during encoding. This result represents strong evidence that eye movements during mental imagery do not constitute a complete reproduction of the oculomotor activity produced during the perceptual encoding process. If there had been such a strong connection, the oculomotor activity in the two phases would have been similar, and this was clearly not the case in Experiments 1 and 2 of Paper III.

The fourth principle identified is that eye movements “to nothing” *have a functional role during mental imagery and memory retrieval*. In other words, manipulation of what participants do with their gaze can alter visualisations and either facilitate or impair retrieval performance. This was shown in Paper III and was more thoroughly specified in Paper IV, where it was also shown that looking at a blank space whose location was congruent with that of the previously encoded information facilitated visuospatial remembering for both visual content and spatial relationships compared with looking at a blank space whose location was not congruent with that of the information encoded.

5.1.1 Evaluation I: scanpath theory

Scanpath theory (Brandt & Stark, 1997) is based on the idea that mental images consist of analog representations generated in a visual buffer (Kosslyn, 1994; Kosslyn et al., 2006) of working memory. It predicts that eye movements during scene recollection will be made to the same locations and follow the same sequential order as during scene encoding. However, the third principle identified above clearly states that eye movements during scene recollection do not constitute a reproduction of the oculomotor activity produced during scene encoding.

Moreover, in Papers I and III it was found that eye movements can reflect spatial content even when visualisation is not preceded by an encoding phase. Consequently, scanpath theory cannot provide a plausible explanation for eye movements “to nothing” during mental imagery.

This, however, does not mean that eye-movement effects during mental imagery cannot be explained by Kosslyn’s visual-buffer model. There are many ways to reconcile results from the studies reported in this thesis with ideas about how information is generated, scanned, inspected or transformed in the visual buffer. For instance, Kosslyn has suggested that eye movements during mental imagery could reflect the process of “sliding” an image in discrete jumps “across” the visual buffer (Kosslyn, 1994, p. 367). However, this suggestion has not been further elaborated upon or investigated.

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What is more, even if participants maintained central fixation during encoding in Experiments 1 and 2, they probably engaged in several covert attention shifts when trying to inspect the picture and possibly even when listening to the scene description. Thomas and Lleras (2009) have shown that covert attention shifts can produce identical results in a problem-solving task as overt eye movements. Therefore it is possible that, despite the maintenance of central fixation, the mechanisms that generate saccades were prepared and programmed during encoding through covert attention shifts (e.g., Deubel & Schneider, 1996; Irwin & Gordon, 1998; Theeuwes et al., 2005). In the subsequent recall phase involving free viewing, then, these covert attention shifts – or these programmed saccades – will have been reproduced, manifesting themselves at that stage as overt eye movements.

5.1.2 Evaluation II: spatial indexes

Pylyshyn’s visual-index theory (e.g., Pylyshyn, 2002) assumes that all internal representations are propositional and that eye movements during mental imagery reflect a procedure where imagined objects are bound to visual features in the outside world (Pylyshyn, 2002, p. 181). However, the second principle identified above (which was based on the complete-darkness experiments) states that eye movements during mental imagery are dependent upon content and spatial relationships of the scene being visualised, not on visual features in the outside world. Visual-index theory cannot explain the results of the complete-darkness experiments.

Nevertheless, there are other accounts of spatial indexing where the “external memory store” (e.g., O’Regan & Noë, 2001) is not the only memory source at hand (e.g., Ballard et al., 1997; Richardson et al., 2009), but internal visuospatial representations can account for an important part of the memory traces activated during scene recollection. This means that, according to this version of spatial-index theory, while eye movements to blank spaces may not be necessary during mental imagery, they can play an important and supportive role in this context. On this view, the cognitive system uses both external and internal memory stores so as to minimise the demands placed on memory, making use of all information available in order to achieve a given goal as efficiently as possible.

Here it could be noted, for example, that the global rate of correspondence was significantly lower for the complete-darkness experiments reported in Paper I than for the blank-screen experiments. Eye movements thus seem to increase in proportion to the amount of support that the outside world can provide. Analogous results were obtained by Spivey and Geng (2000), who reported more eye movements to corresponding locations when the recall phase included the grid from the original encoding phase than when a completely blank screen was used.

This interpretation is further supported by the findings of Paper II, where it was shown that those with poorer spatial-imagery capabilities were more likely to execute eye movements that spread out and corresponded to the original spatial layout of the scene being recalled.

Accounts of this type can very convincingly explain the results from all the studies reported in this thesis (and the corresponding principles as identified above), especially the findings of Paper II relating to individual differences.

5.1.3 Evaluation III: enactive theory and simulation theory

In the enactive theory of imagery (Thomas, 2009), imagery experiences arise when we actively search for information, even if there is nothing to be found. In simulation theory

(e.g., Hesslow, 2012) and grounded cognition (e.g., Barsalou, 2008), imagery experiences arise when we are engaged in a perceptual simulation. In such theories, recalling a scene is similar to actually perceiving the scene, except that there is no perceptual feedback from the scene itself. Consequently, behaviour during visual imagery will be similar to behaviour during visual perception, with eye movements being activated as if the person were actually looking at the scene that he or she is imagining. Further, because of individual differences in how these perceptual simulations are performed, there is also expected to be a great deal of variation among participants – such as that reported in Paper I and especially in Paper II.

It is also worth mentioning that according to enactive theory (Thomas, 2009) and simulation theory (Hesslow, 2012), eye movements during recall do not – as in scanpath theory – reflect a complete reactivation of the oculomotor activity produced during encoding. The term “re-enactment” used in such accounts refer to the re-enactment of visual-perception behaviour in general, not of such behaviour during a specific encoding phase. The results from Experiments 1 and 2 of Paper III, as reflected in the third principle identified above, are therefore not unexpected from the perspective of simulation theory and enactive theory.

Theories of these kinds can thus convincingly explain the results from all of the studies reported in this thesis (and the principles identified on the basis of those results). However, one problem with these theories is that they are very general in nature and can explain any and all results where cognitive processes are activated similarly during mental imagery as during visual perception. In other words, explanatory power is gained at the expense of predictive power. However, largely inspired by enactive theory, Sima (2011) has recently developed a formal model where mental imagery as a phenomenon is explained with reference to covert and overt attention shifts (including specific predictions of how and when eye movements are executed). In this model, eye movements during mental imagery are explained on the basis of different levels of visuospatial processing. For instance, it is argued that detailed visuospatial recollections are more likely to induce overt attention shifts (eye movements) than spatial mental models of a merely schematic nature. The experiments included in this thesis did not investigate such different levels of visuospatial processing and therefore cannot be used to evaluate Sima’s model, but this will be an interesting challenge for future research.

5.1.4 Evaluation IV: memory retrieval

All of the above-mentioned theories predict, at least to some extent, that eye movements “to nothing” during mental imagery can act as facilitatory cues during memory retrieval of scenes and visuospatial information.

The fourth principle identified above states, in rather general terms, that eye movements have a functional role during mental imagery and memory retrieval. Consequently, memory performance can be altered and impaired if eye-movement restrictions are introduced during the recall phase. This is exactly what is predicted by scanpath theory, by spatial indexes (at least on some interpretations) and by enactive and simulation theory. What is more, it was shown in Paper IV that visuospatial remembering can be facilitated when the position of the gaze is manipulated towards an area corresponding to the original location of the object to be recalled. This effect was robust both for the retrieval of intrinsic object features and for the retrieval of spatial relationships between objects. While facilitated memory performance for intrinsic object features is not predicted by Pylyshyn’s visual-index theory, it can be reconciled with other versions of spatial-index theory and

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is explicitly predicted by scanpath theory and enactive/simulation theory. Further, Paper IV also showed that a central-fixation restriction during recall affects performance differently for the retrieval of intrinsic object features and the retrieval of spatial relationships between objects. Such an effect is likely from the perspective of spatial indexes and enactive/simulation theory, where behavioural differences are dependent on individual capabilities, on the cognitive load and on the external support available. By contrast, such a difference in performance is harder to reconcile with scanpath theory, which is less flexible in this respect.

5.1.5 Mental imagery and cognitive science

As stated in the introduction, the overall aim of this thesis is to identify general principles that apply to eye movements during mental imagery and memory retrieval rather than explaining such eye movements with reference to any formal model where the components of mental-imagery processes and mechanisms are explicitly specified (such as, for example, Kosslyn's visual-buffer model). Even so, the attentive reader may have noticed that an embodied account of the mind, where cognition is grounded in modal simulations, motor processes and situated action (e.g., Barsalou, 2008; Hesslow, 2012; Spivey, 2007), is frequently favoured over the traditional, computational-functionalist approach to cognition (for a recent overview of computational functionalism, see Piccinini & Bahar, 2012). This is, of course, no coincidence. I do believe that taking an embodied approach to cognition, where dynamic processes are actively situated in the external environment, and where there are no sharp boundaries between action, perception and cognition, is the most fruitful way forward for cognitive science in general, and for mental-imagery research in particular.

Historically, the clash between analog and propositional accounts within a computational-functionalist framework has played a very important role for the development of mental-imagery research (Kosslyn et al., 2006; Pylyshyn, 2002), especially when it comes to identifying different components that are involved in mental imagery. For instance, in the visual-buffer model as originally drawn up (Kosslyn & Schwartz, 1977; Kosslyn, 1980), separate processes were identified for locating and integrating parts of an image, for reorienting, repositioning and scaling the image, and for preventing the image from fading. Over the years, the visual-buffer model has been fine-tuned to accommodate new empirical findings and neurological discoveries (Kosslyn 1994; Kosslyn et al., 2006), and those conducting research to support this model have provided a great deal of convincing evidence identifying the processes and sub-processes that are active during mental-imagery tasks (see Kosslyn et al., 2006). As a result, the present-day version of the visual-buffer model has a great deal of explanatory power and is able to account for a great deal of the variance found in mental-imagery studies. However, as this model has gained explanatory power, it has inevitably lost predictive power. It may be on its way to becoming so general that it cannot be falsifiable. What is more, with current advances in neuroscience it may also turn out that a formal model originally developed to explain information processing as if it resembled the workings of computer software (e.g., Kosslyn & Schwartz, 1977) may not be ecologically valid given our growing knowledge of how the neurophysiology of the human brain actually works (e.g., Piccinini & Bahar, 2012).

For the future, therefore, I believe that a change of approach is warranted. As I see it, identifying general principles within the framework of an embodied view of the human mind (e.g., Barsalou, 2008), where action, perception and cognition are grounded as mental simulations in a single, dynamic continuum (Spivey, 2007), is a more fruitful

way forward for cognitive science in general and for mental-imagery research in particular. Also, since in many ways the eyes represent the nexus of action, perception and cognition, I believe that eye-movement studies constitute a natural and powerful tool for advancing our conceptual knowledge of mental imagery, attention and memory. This may not seem an entirely obvious conclusion given that, as I have pointed out above, embodied accounts and theories of mental simulations (e.g., Barsalou, 2008; Hesslow, 2012) are also very general in nature and have great explanatory power at the expense of predictive power. I would therefore like to emphasise that the main reason why I prefer the approach of identifying general principles within such a framework is that this approach is more ecologically valid with respect to how we interact, externally and internally, with the physical world around us and, also, that this approach fits better within the neurophysiological constraints of the human organism itself (e.g., Gibson, 1979). In fact, such ecological constraints are not always very well captured by formal models, which historically have been based on a computational-functionalist approach to cognition (e.g., Piccinini & Bahar, 2012). However, it should be mentioned that attempts to merge embodied accounts with computational models have started to appear in recent research (for an overview, see Pezzulo, Barsalou, Cangelosi, Fischer, McRae, & Spivey, 2013).

It is important to point out that taking an embodied and dynamic view of cognition is not by any means revolutionary in contemporary cognitive science. On the contrary, this is probably the most popular view of the mind today (for a recent overview, see Clark, 2012). For instance, even Kosslyn now appears to embrace more embodied and dynamic approaches to cognition and has recently co-authored an article where a conceptual framework for the role of mental imagery is described as a “mental emulation” of perceptual behaviour (Moulton & Kosslyn, 2009).

5.1.6 The perception-imagery relationship revisited

To sum up, through the studies presented in this thesis I have demonstrated that mental-imagery experiences are frequently accompanied by corresponding eye movements, I have specified how such eye movements relate to perceptual encoding and individual capabilities, I have shown that the position of the gaze – even when there is no relevant visual input – can facilitate memory retrieval, and I have found that there are several plausible theoretical explanations for these findings. From a broader perspective, these findings show that eye movements not only serve to provide input to the visual system but are also involved in the top-down processes that give rise to mental-imagery experiences and episodic-memory retrieval. I have presented four principles for how eye movements are associated with those processes, and how they are not. Moreover, I have outlined a general framework for the levels at which imagery processes may be shared with perception, the visual system and the oculomotor system, and how those processes may interact with attention and memory systems. To fully understand this complex interplay, however, much future research is necessary.

Chapter 6

Applications and future directions

Besides providing fundamental knowledge of how eye movements interact with mental-imagery processes and how this can be related to neurocognitive models of the human mind, the results from the studies reported in this thesis can also have important implications for more applied strands of research. For example, it has been shown that the ability to engage in mental imagery has important implications for problem-solving (e.g., Hegarty & Kozhevnikov, 1999), design (e.g., Gero et al., 2001), creative thinking (e.g., Clement, 2008), learning (e.g., Glenberg et al., 2004) and mental practice (e.g., Sevдалис et al., 2013).

Further, eye movements reflecting mental imagery have been reported to occur in various types of more applied research settings. For example, Hegarty (1992) has demonstrated that participants who are trying to understand physical systems make eye movements that reflect “mental animation” of those systems. This has recently been further specified by Eitel, Scheiter, Schüler, Nyström, and Holmqvist (2013), who showed in detail how eye movements reflect mental animation during the construction of a mental model of a physical system. Yoon and Narayanan (2004) reported that participants who were engaged in a problem-solving task frequently executed eye movements towards a blank area where a relevant mechanical device had previously been shown. Similar findings have been reported by Freksa and Bertel (2007) for the solving of diagrammatic problems, by Huber and Kirst (2004) and Kozhevnikov, Motes, and Hegarty (2007) for physics tasks involving judgements of movement, and by Sima, Schultheis and Barkowsky (2013) for the use of mental models during a reasoning task.

Further, Matlock and Richardson (2004) have demonstrated that an eye-movement effect of mental animation is also present for fictive-motion sentences (such as “the road runs through the desert”), and Polunin, Holmqvist, and Johansson (2008) have demonstrated that participants who engage in mental imagery during a task involving statements of time spontaneously move their eyes along a “mental timeline” (events that had happened in the past elicited eye movements further to the left than events that were supposed to happen in the future). Recently, the phenomenon of looking “at nothing” has also been successfully used to trace memory processes and individual strategies in a decision-making task (Renkewitz & Jahn, 2012).

Eye movements “to nothing” thus occur in many types of tasks. A conservative claim in this context is that the empirical findings and methodologies outlined in this thesis could potentially be important for research on learning, reasoning, decision-making, creative thinking, problem-solving and design. In fact, the findings from Papers I and III have already been of importance to several of the above-mentioned studies (Eitel et al., 2013; Freksa & Bertel, 2007; Renkewitz & Jahn, 2012; Sima et al., 2013) as well as to

the development of new methods (Fourtassi et al., 2013). Moreover, the results from Paper II indicate that the performance of eye movements to blank spaces is associated with visuospatial-imagery capabilities. Much research is of course needed to further investigate this relationship, but the results are promising and could potentially be used to develop new tools to enhance individuals' performance on tasks that require specific visuospatial imagery skills. For instance, it has been found that individuals differ greatly in the extent to which they benefit from using graphical visualisations rather than symbolic representations when solving mathematical problems (Jarodzka, Nyström, & Ögren, 2013), and research on medical professionals has shown not only that there is a relationship between visuospatial abilities and performance but also that performance can be trained and enhanced using interactive 3-D visualisations (Hegarty et al., 2007).

Another potential application is in the field of mental practice. Previous research has shown that mental practice of visuospatial and motor skills can enhance performance in sport (e.g., Olsson & Nyberg, 2010), in medical training (e.g., Sevdalis et al., 2013) and in physical therapy as regards the relearning of locomotor skills (Malouin & Richards, 2009). At present, all of the disciplines concerned rely on subjective reports as regards what methods work best and there is a strong demand for more valid, objective measures. Recent research has shown that eye movements "to nothing" occur during motor-imagery tasks as well, meaning that eye-movement studies could potentially be relevant for mental-practice strategies. For instance, it has been shown that eye movements are executed similarly during imagined goal-directed arm and hand movements as during the corresponding real movements (Gueugneau, Crognier, Charalambos, & Papaxanthis, 2008; Heremans, Helsen, & Feys, 2008), and de'Sperati (2003) has shown that eye movements form curved trajectories during mental-rotation tasks and circular-motion imagery.

Another potential field of application is psychiatry, where the use of mental-imagery strategies is an important tool in the treatment of post-traumatic stress disorder (PTSD), schizophrenia, depression and bipolar disorder (e.g., Pearson et al., 2013). Further, Eye Movement Desensitisation and Reprocessing (EMDR) is currently an approved therapeutic method in Sweden for the treatment of PTSD and traumatic memories. EMDR involves patients being instructed to think about their traumatic memories while simultaneously moving their eyes back and forth between left and right. It is claimed that this gradually transforms the traumatic memory into a more normal, declarative memory, while at the same time reducing symptoms of emotional arousal and physical stress (e.g., Bisson, Ehlers, Matthews, Pilling, Richards, & Turner, 2007). It should be emphasised that this method is very controversial and that it is not supported by any theory explaining how such eye movements are connected to the memory systems or how the therapeutic effects arise. This actually represents a research opportunity: since the role of eye movements during the recollection of visual memories has been thoroughly investigated in this thesis, there is a large potential to build upon these results and conduct future studies to investigate whether, and if so how, EMDR treatment actually is related to the oculomotor system or whether the effects obtained using this method are instead due to something else that has no causal relationship to eye movements.

However, the most fascinating potential application for the research presented in this thesis would be to train people in where and how to look in order to remember and visualise information better. There is some previous research in related fields. For instance, Dewhurst (2009) has shown that it is possible to train people in where to direct eye movements in order to increase performance as regards visual search and stimulus discrimination. So far, though, no studies have investigated whether it is also possible to use eye movements to consciously alter how imagined visuospatial information is re-

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trieved from memory. However, the results from Paper IV are very promising for this kind of application. Further, the results obtained by Renkewitz and Jahn (2012), who traced memory processes and individual decision strategies, are very encouraging when it comes to the feasibility of applying this kind of research to complex real-life situations, even though their study did not investigate any causal relationships. In the long term, the research presented in this thesis could therefore be used to develop mnemonic strategies for settings where memories are commonly distorted and inaccurate (e.g. testimony by eyewitnesses). However, it should be noted that in Paper IV the manipulation of gaze position was obtained through instructions included in the experimental design. Further research is needed to identify with greater accuracy what factors are relevant. For example, what is the relationship between the “movement” of the eye and the position of the gaze? Does it matter whether the eye movement is triggered intentionally or unconsciously? Can the same effect be achieved with covert attention shifts? And exactly how do the circumstances of encoding affect the subsequent retrieval processes?

Before moving on to how I intend to continue my research, I would like to take this opportunity to dismiss a myth common in popular psychology and in the pseudo-science known as neurolinguistic programming (NLP), namely that certain eye movements can be used as reliable indicators of lying (e.g., Gray, 1991). The basic idea behind this claim is that eye movements upwards to the right are associated with telling lies while those going upwards to the left are associated with telling the truth. This, in turn, is based on another false assumption about hemispheric specialisation (see Section 2.2.2 above): that processing in the right hemisphere of the brain is associated with imagination (i.e. lies in this context) and that processing in the left hemisphere is associated with logic (i.e. the truth in this context). This myth about lying and lateralised eye movements was systematically exploded in a recent study by Wiseman, Watt, Ten Brinke, Porter, Couper, and Rankin (2012). Now, the reader might wonder what this has to do with the potential applications of the research presented in this thesis. The short answer is, “nothing”. The reason why I would like to bring it to the reader’s attention at this point is that the most common questions I receive whenever I tell people (outside the little community of eye-movement researchers and cognitive scientists) that I investigate eye movements during mental imagery and memory retrieval go along the lines of, “Oh, that sounds exciting, is it like this thing where you look towards the right when you’re lying and to the left when you’re telling the truth? Or was it the other way round? And is this really true?” So, to round this section off, I would like to answer this once and for all by saying, “No, this common belief is not true and it does not have anything to do with my research.” Dixi.

6.1 Future research

In the near future, my research will continue with investigations of the relationship between looking “at nothing” and memory retrieval. The main focus will be to disambiguate the effect of eye “movements”, gaze location, and intentionality, and to tie this relationship closer to current neurocognitive models of memory retrieval. This research will also involve more detailed investigations of how the encoding process predicts subsequent retrieval (which the studies in the present thesis did not investigate). A related avenue down which I will take my research concerns whether looking “at nothing” during recall can also facilitate memory retrieval of information that is not visuospatial per se. For instance, I intend to examine whether it is possible to achieve this effect for verbal memory as well, like in the studies conducted by Richardson et al. (2009), where retrieval instead depended upon linguistic information that had been associated with specific spaces during encoding.

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Recent research by Scholz, Mehlhorn, and Krems (2012) suggests that this may in fact be the case.

Close collaborators of mine have developed, in a recent project (which I have also been a part of – but only to a very small degree), a new method to compare different dimensions of scanpath similarity (shape, position, direction, duration and order) called MultiMatch (Dewhurst, Nyström, Jarodzka, Foulsham, Johansson, & Holmqvist, 2012). Another future endeavour will therefore be to use this method to further explore the relationship between scanpaths during encoding and recall.

Further, a different project that I am involved in will conduct a detailed investigation of the spatial frames of reference used when people look “at nothing” during mental imagery. For instance, we intend to examine to what extent these frames are viewer-based (or egocentric) and to what extent they are scene-based (or allocentric), and how this relates to frames of reference in the external environment (like a computer screen) and to the position of the observer’s own eyes, head and body.

Over the years I have also worked in a completely different project where we investigate the writing process during text production, and specifically how visual feedback from an emerging text affects the writing process and the final text product (e.g., Johansson, Wengelin, Johansson, & Holmqvist, 2010; Wengelin, Torrance, Holmqvist, Simpson, Galbraith, Johansson, & Johansson, 2009). In the future, I hope that I will be able to combine this research with ideas from this thesis and to investigate in detail how look-backs and the spatial representation of the emerging text interact and affect the writer’s visual feedback, memory and plans for future text segments.

Finally, I am also enrolled in a project where we have started to use ideas from the phenomenon of looking “at nothing” to investigate the impact of external and internal information processing during consumers’ decision-making. This project has just started and it is hard to say what results will come out of it. But the study by Renkewitz and Jahn (2012), who successfully traced individual decision strategies through eye movements to blank spaces, is a very encouraging starting-point (see also Gidlöf, Wallin, Dewhurst, & Holmqvist, 2013, for an overview of eye-movement research in the field of consumers’ decision-making).

To sum up, I hope that the empirical and conceptual advances as regards eye movements during mental imagery and memory retrieval which have been presented in this thesis can provide the basis for much new research and that they can be used to inspire and stimulate many future discoveries.

Bibliography

- Albers, A. M., Kok, P., Toni, I., Dijkerman, H. C., & de Lange, F. P. (2013). Shared Representations for Working Memory and Mental Imagery in Early Visual Cortex. *Current Biology*. (Epub ahead of print.).
- Altmann, G. T. M. (2004). Language-mediated eye movements in the absence of a visual world: the 'blank screen paradigm'. *Cognition*, 93 (2), 79-87.
- Altmann, G. T. M., & Kamide, Y. (2009). Discourse-mediation of the mapping between language and the visual world: Eye-movements and mental representation. *Cognition*, 111(1), 55-71.
- Antrobus, J. S., Antrobus, J. S., & Singer, J. L. (1964). Eye movements accompanying daydreaming, visual imagery, and thought suppression. *Journal of Abnormal and Social Psychology*, 69, 244-252.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5(3), 119-126.
- Baddeley, A.D. (1986). *Working Memory*. Oxford: Oxford University Press.
- Bain, A. (1855). *The senses and the intellect*. London, John W. Parker and Son, West Strand.
- Ballard, D. H., Hayhoe, M. M., Pook, P. K., & Rao, R. P. N. (1997). Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences*, 20, 723-767.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22, 577-660.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59(1), 617-645.
- Bartolomeo, P., Bachoud-Lévi, A. C., De Gelder, B., Denes, G., Dalla Barba, G., Brugieres, P., & Degos, J. D. (1998). Multiple-Domain Dissociation between Impaired Visual Perception and Preserved Mental Imagery in a Patient with Bilateral Extrastriate Lesions. *Neuropsychologia*, 36, 239-249.
- Bergen, B., Lindsay, S., Matlock, T., & Narayanan, S. (2007). Spatial and linguistic aspects of visual imagery in sentence comprehension. *Cognitive Science*, 31.
- Bergstrom, K. J., & Hiscock, M. (1988). Factors influencing ocular motility during the performance of cognitive tasks. *Canadian Journal of Psychology*, 42, 1-23.
- Betts, G. H. (1909). *The distribution and functions of mental imagery* (Contributions to Education, No. 26). New York: Columbia University, Teachers College.

- Bisiach, E., & Luzzatti, C. (1978). Unilateral Neglect of Representational Space. *Cortex*, 14, 129-133.
- Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annual review of neuroscience*, 33, 1.
- Bisson, J. I., Ehlers, A., Matthews, R., Pilling, S., Richards, D., & Turner, S. (2007). Psychological treatments for chronic post-traumatic stress disorder Systematic review and meta-analysis. *The British journal of psychiatry*, 190(2), 97-104.
- Blazhenkova, O., & Kozhevnikov, M. (2009). The new object-spatial-verbal cognitive style model: Theory and measurement. *Applied Cognitive Psychology*, 23, 638-663.
- Block, N. (1983). Mental pictures and cognitive science. *The Philosophical Review*, 92(4), 499-541.
- Borst, G., & Kosslyn, S. M. (2008). Visual mental imagery and visual perception: Structural equivalence revealed by scanning processes. *Memory & Cognition*, 36(4), 849-862.
- Borst, G., & Kosslyn, S. M. (2010). Individual differences in spatial mental imagery. *The Quarterly Journal of Experimental Psychology*, 63(10), 2031-2050.
- Bourlon, C., Oliviero, N., Wattiez, P., Pouget, P., & Bartolomeo, P. (2010). Visual mental imagery: What the head's eye tells the mind's eye. *Brain Research*, 1367, 287-297.
- Bower, G. H. (1970). Analysis of a mnemonic device: Modern psychology uncovers the powerful components of an ancient system for improving memory. *American Scientist*, 58(5), 496-510.
- Bower, G. H., & Morrow, D. G. (1990). Mental models in narrative comprehension. *Science*, 247, 44-48.
- Boyer, P. (2008). Evolutionary economics of mental time travel? *Trends in cognitive sciences*, 12(6), 219-224.
- Brandt, S. A., & Stark, L. W. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of Cognitive Neuroscience*, 9, 27-38.
- Brewer, W. F., & Schommer-Aikins, M. (2006). Scientists Are Not Deficient in Mental Imagery: Galton Revised. *Review of General Psychology*, 10, 130-146.
- Brockmole, J. R., & Irwin, D. E. (2005). Eye movements and the integration of visual memory and visual perception. *Perception & Psychophysics*, 67(3), 495-512.
- Brown, B. B. (1968). Visual recall ability and eye movements. *Psychophysiology*, 4, 300-306.
- Chatterjee, A., & Southwood, M. H. (1995). Cortical Blindness and Visual Imagery. *Neurology*, 45, 2189-2195.
- Clark, A. (2012). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, 1-86.

- Clark, H. (1916). Visual imagery and attention: an analytical study. *American Journal of Psychology*, 27(4), 461-492.
- Clement, J. (2008). *Creative Model Construction in Scientists and Students: The Role of Imagery, Analogy, and Mental Simulation*. Dordrecht: Springer.
- Conway, A. R., Kane, M. J., Bunting, M. F., Hambrick, D. Z., Wilhelm, O., & Engle, R. W. (2005). Working memory span tasks: A methodological review and user's guide. *Psychonomic bulletin & review*, 12(5), 769-786.
- Cooper, L. A., & Shepard, R. N. (1973). Chronometric Studies of the Rotation of Mental Images. In W.G. Chase (Ed.), *Visual Information Processing* (pp. 75-176). New York: Academic Press.
- Corbetta, M., & Schulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201-215.
- Currie, G. (1995). Visual Imagery as the Simulation of Vision. *Mind and Language*, 10, 25-44.
- Danker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the brain regions engaged during encoding. *Psychological Bulletin*, 136, 87-102.
- Deckert, G. H. (1964). Pursuit eye movements in the absence of a moving visual stimulus. *Science*, 143, 1192-1193.
- Demarais, A., & Cohen, B. H. (1998). Evidence for image-scanning eye movements during transitive inference. *Biological Psychology*, 49, 229-247.
- Dement W. C. (1964). Eye movements during sleep. In: M. B. Bender (Ed.), *The oculomotor system*, (pp. 366-416). Hoeber, New York.
- Dement, W., & Kleitman, N. (1957). The relation of eye movements during sleep to dream activity: An objective method for the study of dreaming. *Journal of Experimental Psychology: General*, 55, 339-346.
- de'Sperati, C. (2003). Precise oculomotor correlates of visuo-spatial mental rotation and circular motion imagery. *Journal of Cognitive Neuroscience*, 15, 1244-59.
- D'Esposito, M., Detre, J. A., Aguirre, G. K., Stallcup, M., Alsop, D. C., Tippet, L. J., & Farah, M. J. (1997). A Functional MRI Study of Mental Image Generation. *Neuropsychologia*, 35, 725-730.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, 36(12), 1827-1837.
- Dewhurst, R. (2009). *Evaluating strategies for visual search and stimulus discrimination: implications for training eye-movements*. PhD thesis, University of Nottingham.
- Dewhurst, R., Nyström, M., Jarodzka, H., Foulsham, T., Johansson, R., & Holmqvist, K. (2012). It depends on how you look at it: Scanpath comparison in multiple dimensions with MultiMatch, a vector-based approach. *Behavior research methods*, 44(4), 1079-1100.

- Doricchi, F., Iaria, G., Silvetti, M., Figliozzi, F., & Siegler, I. (2007). The "ways" we look at dreams: evidence from unilateral spatial neglect (with an evolutionary account of dream bizarreness). *Experimental brain research*, 178(4), 450-461.
- Ehrlichman, H., & Barrett, J. (1983a). Right hemispheric specialization for mental imagery: A review of the evidence. *Brain and Cognition*, 2(1), 55-76.
- Ehrlichman, H., & Barrett, J. (1983b). "Random" saccadic eye movements during verbal-linguistic and visual-imaginal tasks. *Acta Psychologica*, 53, 9-26.
- Eitel, A., Scheiter, K., Schüler, A., Nyström, M., & Holmqvist, K. (2013). How a picture facilitates the process of learning from text: Evidence for scaffolding. *Learning and Instruction*, 28, 48-63.
- Engle, R. W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, 11, 19-23.
- Farah, M. J. (1988). Is Visual Imagery Really Visual? Overlooked Evidence from Neuropsychology. *Psychological Review*, 95, 307-317.
- Farah, M. J. (2000). *The cognitive neuroscience of vision*. Oxford, UK: Blackwell.
- Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive Psychology*, 20, 439-462.
- Farah, M. J., Peronnet, F., Gonon, M. A., & Girard, M. H. (1988). Electrophysiological evidence for a shared representational medium for visual images and visual percepts. *Journal of Experimental Psychology: General*, 117, 248-257.
- Farah, M. J., Soso, M. J., & Dasheif, R. M. (1992). Visual Angle of the Mind's Eye Before and After Unilateral Occipital Lobectomy. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 241-246.
- Ferreira, F., Apel, A., & Henderson, J. M. (2008). Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, 12(11), 405-410.
- Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision: The psychology of looking and seeing*. Oxford University Press.
- Findlay, J. M., & Walker, R. (1999). How are saccades generated? *Behavioral and Brain Sciences*, 22(4), 706-713.
- Finke, R. A. (1985). Theories relating mental imagery to perception. *Psychological Bulletin*, 98(2), 236-259.
- Finke, R. A. (1986). Mental imagery and the visual system. *Scientific American*, 254, 88-95.
- Finke, R. A. (1989). *Principles of Mental Imagery*. Cambridge, MA: MIT Press.
- Finke, R. A., & Pinker, S. (1983). Directional Scanning of Remembered Visual Patterns. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 9, 398-410.
- Fodor, J. A. (1975). *The language of thought*. Harvard University Press.

- Foulsham, T., & Kingstone, A. (2013). Fixation-dependent memory for natural scenes: An experimental test of scanpath theory. *Journal of Experimental Psychology: General*, 142, 41-56.
- Foulsham, T., & Underwood, G. (2008). What can saliency models predict about eye movements? Spatial and sequential aspects of fixations during encoding and recognition. *Journal of Vision*, 8(2):6, 1-17.
- Fourtassi, M., Hajjioui, A., Urquizar, C., Rossetti, Y., Rode, G., & Pisella, L. (2013). Iterative Fragmentation of Cognitive Maps in a Visual Imagery Task. *PLoS one*, 8(7).
- Fox, P. T., Mintun, M. A., Raichle, M. E., Miezen, F. M., Allman, J. M., & Van Essen, D. C. (1986). Mapping human visual cortex with positron emission tomography. *Nature*, 323, 806-809.
- Freksa, C., & Bertel, S. (2007). Eye movements and smart technology. *Computers in Biology and Medicine*, 37, 983 - 988.
- Galton, F. (1880). Statistics of mental imagery. *Mind*, 5, 301-318.
- Galton, F. (1883). *Inquiries into human faculty and its development*. London: Macmillan.
- Ganis, G., & Schendan, H. E. (2008). Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. *NeuroImage*, 42, 1714-1727.
- Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research*, 20, 226-241.
- Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication Does the corpus callosum enable the human condition? *Brain*, 123(7), 1293-1326.
- Gazzaniga, M. S., Ivry, R., & Mangun, G.R. (2008). *Cognitive Neuroscience: The Biology of the Mind*. W.W. Norton, New York, (3rd Edition).
- Gbadamosi, J., & Zangemeister, W. H. (2001). Visual imagery in hemianopic patients, *Journal of Cognitive Neuroscience*. 13 (7), 45-56.
- Geng, J. J., Ruff, C. C., & Driver, J. (2009). Saccades to a remembered location elicit spatially specific activation in the human retinotopic visual cortex. *Journal of Cognitive Neuroscience*. 21, 230-245.
- Gero, J. S., Tversky, B. T., & Purcell, T. (eds). (2001). *Visual and spatial reasoning in design II. Key Centre of design computing and cognition*. University of Sydney, Sydney.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Gidlöf, K., Wallin, A., Dewhurst, R. & Holmqvist, K. (2013). Using eye tracking to trace a cognitive process: Gaze behaviour during decision making in a natural environment. *Journal of Eye Movement Research*, 6(1):3, 1-14.

- Glenberg, A. M. (1997). What memory is for. *Behavioral Brain Sciences*, 20, 1-55.
- Glenberg, A. M., Gutierrez, T., Levin, J. R., Japuntich, S., & Kaschak, M. P. (2004). Activity and imagined activity can enhance young children's reading comprehension. *Journal of Educational Psychology*, 96, 424-436.
- Godijn, R., & Theeuwes, J. (2012). Overt is no better than covert when rehearsing visuo-spatial information in working memory. *Memory & Cognition*, 40(1), 52-61.
- Goldberg, J. H., & Kotval, X. P. (1999). Computer interface evaluation using eye movements: Methods and construct. *International Journal of Industrial Ergonomics*, 24(6), 631-645.
- Goldthwait, C. (1933). Relation of eye movements to visual imagery. *American Journal of Psychology*, 45, 106-110.
- Goodwin, G. P., & Johnson-Laird, P. N. (2005) Reasoning about relations. *Psychological Review*, 112, 479-490.
- Gray, R. (1991). Tools for the trade: Neuro-linguistic programming and the art of communication. *Federal Probation*, 55, 11-16.
- Gueugneau, N., Crognier, L., & Papaxanthis, C. (2008). The influence of eye movements on the temporal features of executed and imagined arm movements. *Brain research*, 1187, 95-102.
- Hale, S. M., & Simpson, H. M. (1971). Effects of eye movements on the rate of discovery and the vividness of visual images. *Perception & Psychophysics*, 9(2), 242-246.
- Hall, D. C. (1974). Eye movements in scanning iconic imagery. *Journal of Experimental Psychology*, 103(5), 925-830.
- Hebb, D. O. (1968). Concerning imagery. *Psychological Review*, 75, 466-477.
- Hegarty, M. (1992). Mental animation: Inferring motion from static displays of mechanical systems. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18, 1084-1102.
- Hegarty, M. (2004). Mechanical reasoning by mental simulation. *Trends in Cognitive Sciences*, 8, 280-285.
- Hegarty, M., & Kozhevnikov, M. (1999). Types of visual-spatial representations and mathematical problem solving. *Journal of Educational Psychology*, 91, 684-689.
- Henderson, J. M., & Ferreira, F. (2004). Scene perception for psycholinguists. In J. M. Henderson & F. Ferreira (Eds.), *The Interface of Language, Vision, and Action: Eye Movements and the Visual World* (pp. 1-58). New York: Psychology Press.
- Henderson, J., Pollatsek, A., & Rayner, K. (1989). Covert visual attention and extrafoveal information use during object identification. *Perception and Psychophysics*, 57, 787-795.

- Heremans, E., Nieuwboer, A., Feys, P., Vercruyssen, S., Vandenberghe, W., Sharma, N., & Helsen, W. F. (2012). External cueing improves motor imagery quality in patients with Parkinson disease. *Neurorehabilitation and neural repair*, 26(1), 27-35.
- Herman, J. H., Barker, D. R., & Roffwarg, H. (1983). Similarity of eye movements characteristics in REM sleep and the awake state. *Psychophysiology*, 20, 537-543.
- Hesslow, G. (2002). Conscious Thought as Simulation of Behaviour and Perception. *Trends in Cognitive Sciences*, 6, 242-247.
- Hesslow, G. (2012). The current status of the simulation theory of cognition. *Brain research*, 1428, 71-79.
- Hiscock, M., & Bergstrom, K. J. (1981). Ocular motility as an indicator of verbal and visuospatial processing. *Memory and Cognition*, 9, 332-338.
- Hollingworth, A. (2006). Scene and position specificity in visual memory for objects. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 32, 58-69.
- Holm, L., & Mäntylä, T. (2007). Memory for scenes: Refixations reflect retrieval. *Memory & Cognition*, 35, 1664-1674.
- Holmqvist, K., Nyström, M., Andersson, R., Dewhurst, R., Jarodzka, H., & van de Weijer, J. (2011). *Eye tracking: a comprehensive guide to methods and measures*. Oxford University Press.
- Holsanova, J., Hedberg, B., & Nilsson, N. (1999). Visual and Verbal Focus Patterns when Describing Pictures. In Becker, Deubel & Mergner (Eds.), *Current Oculomotor Research: Physiological and Psychological Aspects*. Plenum: New York, London, Moscow.
- Holsanova, J. (2001). *Picture Viewing and Picture Description: Two Windows on the Mind*. Doctoral dissertation. Lund University Cognitive Studies 83. ISSN 1101-8453. ISBN 91-856843-76.
- Holsanova, J. (2008). *Discourse, vision, and cognition*. Human Cognitive Processes 23. John Benjamins Publishing Company: Amsterdam/Philadelphia.
- Hooge, I. T. C., & Erkelens, C. J. (1996). Control of fixation duration in a simple search task. *Perception and Psychophysics*, 58, 969-976.
- Hoover, M. A., & Richardson, D. C. (2008). When facts go down the rabbit hole: Contrasting features and objecthood as indexes to memory. *Cognition*, 108, 533-542.
- Huber, S., & Krist, H. (2004). When is the ball going to hit the ground? Duration estimates, eye movements, and mental imagery of object motion. *Journal of Experimental Psychology: Human Perception and Performance*, 30(3), 431-444.
- Huijbers, W., Pennartz, C. M., Rubin, D. C., & Daselaar, S. M. (2011). Imagery and retrieval of auditory and visual information: neural correlates of successful and unsuccessful performance. *Neuropsychologica*, 49(7), 1730-1740.

- Humphrey, K., & Underwood, G. (2008). Fixation sequences in imagery and in recognition during the processing of pictures of real-world scenes. *Journal of Eye Movement Research*, 2(2):3, 1-15.
- Humphrey, K., & Underwood, G. (2011). See What I'm Saying? Expertise and Verbalisation in Perception and Imagery of Complex Scenes. *Cognitive Computation*, 3(1), 64-78.
- Intons-Peterson, M. J. (1983). Imagery paradigms: How vulnerable are they to experimenters' expectations? *Journal of Experimental Psychology: Human Perception & Performance*, 9, 394-412.
- Irwin, D. E. (1996). Integrating information across saccadic eye movements. *Current Directions in Psychological Science*, 5, 94-100.
- Irwin, D. E., & Gordon, R. D. (1998). Eye movements, attention and trans-saccadic memory. *Visual Cognition*, 5(1-2), 127-155.
- Ishai, A., & Sagi, D. (1995). Common mechanisms of visual imagery and perception. *Science*, 268, 1772-1774.
- Itti, L. (2006). Quantitative modeling of perceptual salience at human eye position. *Visual Cognition*, 14(4-8), 959-984.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2, 194-203.
- Jacobs, L., Feldman, M., & Bender, M. B. (1972). Are the eye movements of dreaming sleep related to the visual images of the dreams? *Psychophysiology*, 9, 393-401.
- Jacobson, E. (1932). Electrophysiology of mental activities. *American Journal of Psychology*, 44, 677-694.
- James, W. (1890). *The Principles of Psychology*. New York: Holt. Harvard University Press edition of 1983.
- Janssen, W. H., Nodine, C. F. (1974). Eye movements and visual imagery in free recall. *Acta Psychologica*, 38, 267-276.
- Jarodzka, H., Nyström, M., & Ögren, M. (2013). There's more to multimedia than meets the eye: is seeing pictures believing? *Proceedings of the 17th European Conference on Eye Movements* (p. 208).
- Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *Journal of Experimental Psychology: Human Perception & Performance*, 38, 1289-1314.
- Johansson, R., Holsanova, J., & Holmqvist, K. (2006). Pictures and spoken descriptions elicit similar eye movements during mental imagery, both in light and in complete darkness. *Cognitive Science*, 30(6), 1053-1079.
- Johansson, R., Holsanova, J., & Holmqvist, K. (2011). The dispersion of eye movements during visual imagery is related to individual differences in spatial imagery ability. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd*

- Annual Meeting of the Cognitive Science Society* (pp. 1200-1205). Austin, TX: Cognitive Science Society.
- Johansson, R., & Johansson, M. (in press). Look here, eye movements play a functional role in memory retrieval. *Psychological Science*.
- Johansson, R., Wengelin, Å., Johansson, V., & Holmqvist, K. (2010). Looking at the keyboard or the monitor: relationship with text production processes. *Reading and Writing*, 23(7), 835-851.
- Johnston, K., & Everling, S. (2011). Frontal cortex and flexible control of saccades. In: S. P. Liversedge, I. D. Gilchrist, & S. Everling. (Eds.), *The Oxford handbook of eye movements* (279-302). Oxford, UK: Oxford University Press.
- Just, M. A., & Carpenter, P. A. (1980). A theory of reading: From eye fixations to comprehension. *Psychological Review*, 87(4), 329-354.
- Kane, M. J., Bleckley, M. K., Conway, A. R. A., & Engle, R. W. (2001). A controlled-attention view of working-memory capacity. *Journal of Experimental Psychology: General*, 130, 169-183.
- Kent, C., & Lamberts, K. (2008). The encoding-retrieval relationship: retrieval as mental simulation. *Trends in Cognitive Sciences*, 12(3), 92-98.
- Khader, P., Knoth, K., Burke, M., Ranganath, C., Bien, S., & Rosler, F. (2007). Topography and dynamics of associative long-term memory retrieval in humans. *Journal of Cognitive Neuroscience*, 19, 493-512.
- Kahnemann, D., & Tversky, A. (1982) The simulation heuristic. In D. Kahnemann, P. Slovic, & A. Tversky (Eds.), *Judgement under uncertainty: Heuristics and biases*, (pp. 201-208). Cambridge, UK: Cambridge University Press.
- Knoeferle, P., & Crocker, M. W. (2007). The influence of recent scene events on spoken comprehension: Evidence from eye movements. *Journal of Memory and Language*, 57, 519-543.
- Kosslyn, S. M. (1973). Scanning Visual Images: Some Structural Implications. *Perception and Psychophysics*, 14, 90-94.
- Kosslyn, S. M. (1975). Information representation in visual images. *Cognitive Psychology*, 7, 341-370.
- Kosslyn, S. M. (1980). *Image and mind*. Cambridge, MA: Harvard University press.
- Kosslyn, S. M. (1994). *Image and brain*. Cambridge, MA: MIT Press.
- Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual Images Preserve Metric Spatial Information: Evidence from Studies of Image Scanning. *Journal of Experimental Psychology: Human Perception and Performance*, 4, 47-60.
- Kosslyn, S. M., Cave, C. B., Provost, D., & Von Gierke, S. (1988). Sequential processes in image generation. *Cognitive Psychology*, 20, 319-343.

- Kosslyn, S. M., Holtzman, J. D., Farah, M. J., & Gazzaniga, M. S. (1985). A computational analysis of mental image generation: Evidence from functional dissociations in split-brain patients. *Journal of Experimental Psychology: General*, 114(3), 311.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposana, S., Keenan, J. P., Thompson, W. L., Ganis, G., Sukel, K. E., & Alpert, N. M. (1999). The Role of Area 17 in Visual Imagery: Convergent Evidence from PET and rTMS. *Science*, 284, 167-170.
- Kosslyn, S. M., & Shwartz, S. P. (1977). A simulation of visual imagery. *Cognitive Science*, 1, 265-295.
- Kosslyn, S. M., Thompson, W. L., & Alpert, N. M. (1997). Neural systems shared by visual imagery and visual perception: A positron emission tomography study. *NeuroImage*, 6, 320-334.
- Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery*. New York, NY: Oxford University Press.
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378, 496-498.
- Kowler, E. (2011). Eye movements: The past 25 years. *Vision research*, 51(13), 1457-1483.
- Kozhevnikov, M. (2007). Cognitive styles in the context of modern psychology: Toward an integrated framework of cognitive style. *Psychological Bulletin*, 133(3), 464-481.
- Kozhevnikov, M., Blazhenkova, O., & Becker, M. (2010). Trade-off in object versus spatial visualization abilities: Restriction in the development of visual-processing resources. *Psychonomic Bulletin & Review*, 17(1), 29-35.
- Kozhevnikov, M., Kosslyn, S., & Shephard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory & Cognition*, 33, 710-726.
- Kozhevnikov, M., Motes, M. A., & Hegarty, M. (2007). Spatial visualization in physics problem solving. *Cognitive Science*, 31, 549-579.
- Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, 12(4), 217-230.
- Ladd, G. T. (1892). Contribution to the psychology of visual dreams. *Mind*, 1, 299-304.
- Laeng, B., & Teodorescu, D.-S. (2002). Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cognitive Science*, 26, 207-231.
- Le Bihan, D., Turner, R., Zeffiro, T. A., Cuenod, C. A., Jezzard, P., & Bonnerot, V. (1993). Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study. *Proceedings of the National Academy of Sciences*, 90, 11802-11805.

- Levenshtein, V. I. (1966). Binary codes capable of correcting deletions, insertions and reversals. *Soviet Physics - Doklady*, 10, 707-710).
- Liman, T. G., & Zangemeister, W. H. (2012). Scanpath Eye Movements during Visual Mental Imagery in a Simulated Hemianopia Paradigm. *Journal of Eye Movement Research*, 5(1):2, 1-11.
- Lorenceanu, J. (2012). Cursive Writing with Smooth Pursuit Eye Movements. *Current Biology*, 22, 1506-1509.
- Lorens, S. A., & Darrow, C. W. (1962). Eye movements, EEG, GSR and EKG during mental multiplication. *Electroencephalography & Clinical Neurophysiology*, 14, 739-746.
- Malouin F., & Richards C. L. (2010). Mental practice for relearning locomotor skills. *Physical Therapy*, 90, 240-51.
- Mäntylä, T., & Holm, L. (2006). Gaze control and recollective experience in face recognition. *Visual Cognition*, 14, 365-386.
- Marks, D. F. (1973a). Visual imagery differences and eye movements in the recall of pictures. *Perception & Psychophysics*, 14(3), 407-412.
- Marks, D. F. (1973b). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, 64, 17-24.
- Marr, D. (1971). Simple memory: a theory for archicortex. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 262, 23-81.
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. Cambridge, MA: MIT Press.
- Martarelli, C. S., & Mast, F. W. (2011). Preschool children's eye movements during pictorial recall. *British Journal of Developmental Psychology*, 29, 425-436.
- Martarelli, C. S., & Mast, F. W. (2013). Eye movements during long-term pictorial recall. *Psychological Research*, 77(3), 303-309.
- Mast, F. W., & Kosslyn, S. M. (2002). Eye movements during visual mental imagery. *Trends in Cognitive Sciences*, 6, 271-272.
- Matlock, T. (2004). Fictive motion as cognitive simulation. *Memory & Cognition*, 32(8), 1389-1400.
- Matlock, T., & Richardson, D. C. (2004). Do eye movements go with fictive motion? In *Proceedings of the 26th Annual Meeting of the Cognitive Science Society* (pp. 909-914). Mahwah, NJ: Erlbaum.
- Miller, G. A. (2003). The cognitive revolution: A historical perspective. *Trends in Cognitive Sciences*, 7, 141-144.
- Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.
- Moore, C. S. (1903). Control of the memory image. *Psychological review*, 4, 277-306.

- Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, 16, 519-533.
- Moskowitz, E., & Berger, R. J. (1969). Rapid eye movements and dream imagery: Are they related? *Nature*, 224, 613-614.
- Moulton S. T., & Kosslyn S. M. (2009). Imagining predictions: mental imagery as mental emulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1273–1280.
- Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychological Review*, 110, 611-646.
- Noton, D., & Stark, L. (1971a). Scanpaths in saccadic eye movements while viewing and recognizing patterns. *Vision Research*, 11, 929-942.
- Noton, D., & Stark, L. W. (1971b). Scanpaths in eye movements during perception. *Science*, 171, 308-311.
- Olsson C.-J., & Nyberg L. (2010). Motor imagery: if you can't do it, you won't think it. *Scandinavian Journal of Medicine & Science in Sports*, 20, 711-715.
- O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24, 939-1031.
- Paivio, A. (1971). *Imagery and Verbal Processes*. New York: Holt, Rinehart and Winston.
- Paré, M., & Dorris, M. C. (2011). Role of Posterior Parietal Cortex in the Regulation of Saccadic Eye Movements. In: S. P. Liversedge, I. D. Gilchrist, & S. Everling. (Eds.), *The Oxford handbook of eye movements* (257-278). Oxford, UK: Oxford University Press.
- Parthemore, J., & Morse, A. (2010). Representations reclaimed: Accounting for the co-emergence of concepts and experience. *Pragmatics & Cognition*, 18, 273-312.
- Pearson, D. G., Deeprose, C., Wallace-Hadrill, S. M. A., Burnett Heyes, S., & Holmes, E. A. (2013). Assessing mental imagery in clinical psychology: A review of imagery measures and a guiding framework. *Clinical Psychology Review*, 33, 1-23.
- Perky, C. W. (1910). An experimental study of imagination. *American Journal of Psychology*, 21, 422-452.
- Pezzulo, G., Barsalou, L. W., Cangelosi, A., Fischer, M. H., McRae, K., & Spivey, M. J. (2012). Computational grounded cognition: a new alliance between grounded cognition and computational modeling. *Frontiers in psychology*, 3.
- Piccinini, G., & Bahar, S. (2012). Neural computation and the computational theory of cognition. *Cognitive science*. 37(3), 1-36.

- Podgorny, P., & Shepard, R. N. (1978). Functional Representations Common to Visual Perception and Imagination. *Journal of Experimental Psychology: Human Perception and Performance*, 4, 21-35.
- Pollatsek, A., Rayner, K., & Henderson, J. M. (1990). Role of spatial location in integration of pictorial information across saccades. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 199-210.
- Polunin, O., Holmqvist, K., & Johansson, R. (2008). The time line is mapped onto the visual field. *International Journal of Psychology*, 43(3-4), 610.
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 32(1), 3-25.
- Postle, B. R., Idzikowski, C., Della Salla, S., Logie, R. H., & Baddeley, A. D. (2006). The selective disruption of spatial working memory by eye movements. *Quarterly Journal of Experimental Psychology*, 59(1), 100-120.
- Pylyshyn, Z. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, 87, 16-45.
- Pylyshyn, Z. W. (2002). Mental imagery: In search of a theory. *Behavioral and brain sciences*, 25(2), 157-238.
- Pylyshyn, Z. W. (2003). Return of the mental image: Are there really pictures in the brain? *Trends in Cognitive Sciences*, 7, 113-118.
- Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, 124(3), 372-422.
- Renkewitz, F., & Jahn, G. (2012). Memory indexing: A novel method for tracing memory processes in complex cognitive tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 38(6), 1622-1639.
- Richardson, J. T. E. (1999). *Imagery*. Hove, UK: Psychology Press.
- Richardson, D. C., Altmann, G. T. M., Spivey, M. J., & Hoover, M. A. (2009). Much ado about eye movements to nothing: a response to Ferreira et al.: Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, 13(6), 235-236.
- Richardson, D. C., & Kirkham, N. Z. (2004). Multimodal Events and Moving Locations: Eye Movements of Adults and 6-Month-Olds Reveal Dynamic Spatial Indexing. *Journal of Experimental Psychology: General*, 133(1), 46-62.
- Richardson, D. C., & Spivey, M. J. (2000). Representation, space and Hollywood Squares: looking at things that aren't there anymore. *Cognition*, 76, 269-295.
- Richardson, D. C., Spivey, M. J., Barsalou, L. W., McRae, K. (2003). Spatial representations activated during real-time comprehension of verbs. *Cognitive Science*, 27, 767-780.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25, 31-40.

- Roediger, H. L., III, & Gynn, M. J. (1996). Retrieval processes. In E. L. Bjork & R. A. Bjork (Eds.), *Memory* (pp. 197-236). San Diego: Academic Press.
- Rolfs, M. (2009). Microsaccades: Small steps on a long way. *Vision Research*, 49, 2415-2441.
- Rubin. D. C. (2006). The basic-systems model of episodic memory. *Perspectives on Psychological Science*, 1, 277-311.
- Rugg, M. D., Johnson J. D., Park, H., & Uncapher M. R. (2008). Encoding-retrieval overlap in human episodic memory: a functional neuroimaging perspective. *Progress in Brain Research*, 169, 339-352.
- Schneider, W. X., & Deubel, H. (1995). Visual attention and saccadic eye movements: Evidence for obligatory and selective spatial coupling. In J.M. Findlay, R.W. Kentridge and R. Walker (Eds.), *Eye Movement Research: Mechanisms, Processes and Applications*. Amsterdam: Elsevier Science, pp. 317-324.
- Scholz, A., Melhorn, K., Bocklisch, F., & Krems, J. F. (2011). Looking at nothing diminishes with practice. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd Annual Meeting of the Cognitive Science Society* (pp. 1070-1075). Austin, TX: Cognitive Science Society.
- Scholz, A., Mehlhorn, K., & Krems, J. F. (2012). Looking at nothing facilitates memory retrieval. In N. Miyake, D. Peebles, & R. P. Cooper (Eds.), *Proceedings of the 34th Annual Conference of the Cognitive Science Society* (p. 2855). Austin, TX: Cognitive Science Society.
- Segal, S. J. (1972). Assimilation of a Stimulus in the Construction of an Image: The Perky Effect Revisited. In P.W. Sheehan (Ed.), *The Function and nature of Imagery*, (pp. 203-230). New York & London: Academic Press.
- Sevdalis, N., Moran, A., & Arora, S. (2013). Mental imagery and mental practice applications in surgery: state of the art and future directions. In Lacey, S., & Lawson, R. (Eds.) *Multisensory Imagery*, pp. 343-363, New York, Springer.
- Sheehan, P. W. (1967). A shortened form of the Betts' Questionnaire Upon Mental Imagery. *Journal of Clinical Psychology*, 23, 386-389.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, 98, 507-522.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *The Quarterly Journal of Experimental Psychology*, 38(3), 475-491.
- Shepard, R. N., & Metzler, J. (1971). Mental Rotation of Three-Dimensional Objects. *Science*, 171, 701-703.
- Shimamura, A. P. (2000). The role of the prefrontal cortex in dynamic filtering. *Psychobiology*, 28, 207-218.
- Sima, J. F. (2011). The nature of mental images-an integrative computational theory. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd Annual Meeting of the Cognitive Science Society* (pp. 2878-2883). Austin, TX: Cognitive Science Society.

- Sima, J. F., Schultheis, H., & Barkowsky, T. (2013). Differences between spatial and visual mental representations. *Frontiers in psychology*, 4.
- Skinner, B. F. (1974). *About Behaviorism*. New York: Knopf.
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual Mental Imagery Induces Retinotopically Organized Activation of Early Visual Areas. *Cerebral Cortex*, 15, 1570-1583.
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2012). Visual memory and visual mental imagery recruit common control and sensory regions of the brain. *Cognitive Neuroscience*, 3, 14-20.
- Spivey, M., & Geng, J. (2001). Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychological Research*, 65, 235-241.
- Spivey, M., Tyler, M., Richardson, D., & Young, E. (2000). Eye movements during comprehension of spoken scene descriptions. *Proceedings of the 22nd Annual Conference of the Cognitive Science Society* (pp. 487-492). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.
- Sprenger, A., Lappe-Osthege, M., Talamo, S., Gais, S., Kimmig, H., & Helmchen, C. (2010). Eye movements during REM sleep and imagination of visual scenes. *Neuroreport*, 21(1), 45-49.
- Stoy, E. G. (1930). A preliminary study of ocular attitudes in thinking of spatial relations. *Journal of General Psychology*, 4, 379-385.
- Tanenhaus, M. K., Spivey-Knowlton, M. J., Eberhard, K. M., & Sedivy, J. C. (1995). Integration of visual and linguistic information in spoken language comprehension. *Science*, 268(5217), 1632-1634.
- Theeuwes, J., Belopolsky, A., & Olivers, C. N. L. (2009). Interactions between working memory, attention and eye movements. *Acta Psychologica*, 132(2), 106-114.
- Theeuwes, J., Kramer, A.F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: capture of the eyes by new objects. *Psychological Science*, 9, 379-385.
- Theeuwes, J., Olivers, C. N. L., & Chizk, C. L. (2005). Remembering a location makes the eyes curve away. *Psychological Science*, 16(3), 196-199.
- Thomas, N. J. T. (1999). Are theories of imagery theories of imagination? An active perception approach to conscious mental content. *Cognitive Science*, 23, 207-245.
- Thomas, N. J. T. (2009). Visual Imagery and Consciousness. In W.P. Banks (Ed.), *Encyclopedia of Consciousness* (volume 2, pp. 445-457). Oxford: Elsevier/Academic Press.
- Thomas, N. J. T. (2010). Mental Imagery. In E.N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2010 edition). Online publication: <http://plato.stanford.edu/entries/mental-imagery/>
- Thomas, L. E., & Lleras, A. (2009). Covert shifts of attention function as an implicit aid to insight. *Cognition*, 111(2), 168-174.

- Tootell, R. B., Silverman, M. S., Switkes, E., & de Valois, R. L. (1982). Deoxyglucose analysis of retinotopic organization in primate striate cortex. *Science*, 218(4575), 902-904.
- Totten, E. (1935). *Eye movement during visual imagery*. Comparative Psychology Monographs, 11, 46.
- Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin & Review*, 13(3), 425-457.
- Tulving, E. (1983). *Elements of Episodic Memory*. Oxford, England: Clarendon Press.
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, 80, 352-373.
- Underwood, G., Foulsham, T., van Loon, E., Humphreys, L., & Bloyce, J. (2006). Eye movements during scene inspection: A test of the saliency map hypothesis. *European Journal of Cognitive Psychology*, 18(3), 321-342.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549-586). Cambridge, MA: MIT Press.
- Unsworth, N., Heitz, R. P., Shrock, J. C., & Engle, R. W. (2005). An automated version of the operation span task. *Behavior Research Methods, Instruments, & Computers*, 37, 498-505.
- Van Gog, T., Paas, F., & Van Merriënboer, J. J. G. (2005). Uncovering expertise-related differences in troubleshooting performance: Combining eye movement and concurrent verbal protocol data. *Applied Cognitive Psychology*, 19(2), 205-221.
- Watson, J. B. (1913). Image and Affection in Behavior. *Journal of Philosophy, Psychology and Scientific Methods*, 10, 421-428.
- Weiner, S. L., & Ehrlichman, H. (1976). Ocular motility and cognitive process. *Cognition*, 4, 31-43.
- Wengelin, Å., Torrance, M., Holmqvist, K., Simpson, S., Galbraith, D., Johansson, V., & Johansson, R. (2009). Combined eyetracking and keystroke-logging methods for studying cognitive processes in text production. *Behavior research methods*, 41(2), 337-351.
- Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences*, 97, 11125-11129.
- White, B. J., & Munoz, D. P. (2011). The superior colliculus. In: S. P. Liversedge, I. D. Gilchrist, & S. Everling. (Eds.), *The Oxford handbook of eye movements* (195-213). Oxford, UK: Oxford University Press.
- Wiseman, R., Watt, C., Ten Brinke, L., Porter, S., Couper, S. L., & Rankin, C. (2012). The eyes don't have it: lie detection and neuro-linguistic programming. *PloS one*, 7(7).

- Wolfe, J. M. (1998). Visual search: A review. In H. Pashler (Ed.), *Attention*. London: University College London Press.
- Wooding, D. S. (2002). Fixation maps: quantifying eye-movement traces. *Proceedings of the 2002 symposium on Eye tracking research & applications*, New Orleans, Louisiana.
- Wundt, W. (1912). *An Introduction to Psychology* (2nd edn.). New York: Macmillan. (Translated from the German.).
- Yarbus, A. L. (1967). *Eye Movements and Vision*. New York: Plenum Press.
- Yates, F. A. (1966). *The art of memory*. London: Routledge & Kegan Paul.
- Yoon, D., & Narayanan, N. H. (2004). Mental imagery in problem solving: An eye tracking study. *Proceedings of the Third ACM Symposium on Eye Tracking Research & Applications, Association for Computing Machinery*, ACM Press pp. 77-83.
- Zangemeister, W. H., & Liman, T. (2007). Foveal versus parafoveal scanpaths of visual imagery in virtual hemianopic subjects. *Computers in biology and medicine*, 37(7), 975-982.
- Zirkmund, V. (1972). Physiological correlates of visual imagery. In P. W. Sheehan, (Ed.), *The Function and Nature of Imagery*. New York: Academic Press.

