Bottom-up and top-down selection in time

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The visual environment contains a vast amount of information, most of which is irrelevant for our current goals. Still, we need to be able to select the part that is necessary to act purposefully. This means that the brain faces the difficult task of extracting only the relevant and discarding the irrelevant information. It accomplishes this using a mechanism called selective attention (see e.g. Broadbent, 1982; Johnston & Dark, 1986; Posner & Presti, 1987, for reviews). Selective attention prioritizes some stimuli in the visual field over others, such that they are processed with more resources (Eriksen & Hoffman, 1972; Moran & Desimone, 1985; Mangun, Buonocore, Girelli, & Jha, 1998). Selective attention is assumed to be controlled by two mechanisms: Bottom-up and top-down selection (Treisman & Gelade, 1980; Duncan & Humphreys, 1989; Egeth & Yantis, 1997). Bottom-up selection is stimulus-driven; it prioritizes stimuli that are salient relative to their local surroundings (Koch & Ullman, 1985; Nothdurft, 2002). These stimuli might, for example, have a unique color or orientation, move among static surrounding elements, or differ in size relative to the other stimuli (Wolfe & Horowitz, 2004). Top-down selection is goal-driven. It prioritizes stimuli that are in line with our current behavioral goals (e.g. Posner, 1980).

Bottom-up selection is often assumed to be accomplished on the basis of a salience map (Koch & Ullman, 1985; Itti, 2000; Itti & Koch, 2001). This map is a topographical representation of the relative salience of locations in the visual field. It is computed from several feature conspicuity maps, in which the relative differences within one specific dimension, such as color or orientation, are represented (Itti, Koch, & Niebur, 1998). Competition within the salience map then yields one most salient location that will be selected in a stimulus-driven fashion.

Top-down selection is often thought to require a target template in working memory (e.g. Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). This template biases attentional selection towards objects in the visual field that share a feature with the target. Thus, bottom-up and top-down selection do not necessarily prefer the same stimulus. As a consequence, one of the mechanisms often prevails over the other, as for example in the case of attentional capture where bottom-up selection dominates top-down selection.
Introduction

(Theeuwes, 1992). Here, attention is involuntarily drawn to a salient stimulus, which delays the selection of stimuli that are less salient, but in line with current goal settings. Conversely, goal-driven selection can also dominate stimulus-driven attention, for example, when salient stimuli are actively ignored (Bacon & Egeth, 1994; Yantis & Egeth, 1999).

Both bottom-up and top-down selection can be either spatial (e.g. Posner, 1980; Yantis, 1998) or feature-based (e.g. Rossi & Paradiso, 1995; Treue & Trujillo, 1999; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006). Spatial selection involves the selection of a stimulus at a specific location, for example an object presented on the left side of a display. A typical example for top-down feature-based selection is the selection of a specific color that does not stand out in a bottom-up fashion from the other colors that are present in the visual field. For example, a red target item can be very efficiently found among heterogenously colored and isoluminant distractors, even though it is not salient (Duncan, 1989; Wolfe, Stewart, Friedmanhill, Yu, Shorter, & Cave, 1990). Other features that that have been shown to guide top-down selection are motion, orientation and size (Wolfe & Horowitz, 2004). In contrast to spatial selection, which activates local regions in the visual cortex (e.g. Brefczynski & DeYoe, 1999; Munneke, Heslenfeld, & Theeuwes, 2008), feature-based selection concurs with the activation of neurons with large receptive fields, covering large parts the visual field (Saenz, Buracas, & Boynton, 2002).

To sum up, visual selection can be bottom-up, top-down, location-based and feature-based. This brings up several questions as to how these different aspects of attentional selection interact. For instance, how does bottom-up and top-down selection work? Do bottom-up and top-down selection affect each other, and if yes, how? How are the other two main factors, locations and features, factored into the selection process? There are several classic theories of attentional selection that have provided slightly different answers to these questions.

According to the original Feature Integration Theory (FIT) by Treisman (Treisman, Sykes, & Gelade, 1977; Treisman & Gelade, 1980; Treisman, 1988) visual information is initially analyzed in parallel into separate features (e.g. red or horizontal) which are subsequently represented in different feature maps. Information derived from the individual feature maps can eventually be integrated in a master map of locations through the operation of the “spotlight of attention” (Posner, 1980). Attention serves the purpose of locating and integrating individual, bottom-up generated, features into distinct objects in space. In the original FIT, the spotlight of attention cannot be be top-down guided by any task-relevant feature. The more recent version of FIT (Treisman & Sato, 1990) does allow top-down guidance in that features that do not belong to the current search target are inhibited in a top-down fashion, which facilitates the selection of the target. The Guided Search model (Wolfe, Cave, & Franzel, 1989; Wolfe, 1994) is similar to FIT except that top-down guidance occurs through activation of relevant features instead of inhibition. Biased Competition by Desimone and Duncan (1995) assumes that objects in the visual field directly compete for processing resources, i.e. for representation by the neurons in whose receptive field they are. This competition is biased by stimulus-driven factors, such as the ob-
jects' salience, and top-down factors, such as a target template. This template may also include information about the expected location of an object.

These theories have often been investigated using visual search tasks. In a typical experiment, a search display containing at least one target item and multiple distractors is presented to an observer, who has the task to find the target(s) either covertly (i.e. while retaining fixation at a specified location in the display) or overtly (i.e. looking around using eye movements). These two types of visual selection, i.e. covert and overt selection, have been shown to be closely related (e.g. Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Corbetta, Akbudak, Conturo, Snyder, Ollinger, Drury, Linenweber, Petersen, Raichle, & Vanessen, 1998; Findlay, 2009). The observer then indicates that he/she has found the target by e.g. pressing a response key or making an eye movement to the target. Typical dependent variables are the response time (RT) from search display onset to the key press or eye movement and the accuracy of the response.

In the studies collected in the present thesis, we investigated visual selection using manual reaction times in experiments in which participants had to covertly select a search target (Chapters 2 and 4), as well as the latencies and further properties of overt eye movements to a target element (Chapters 3 and 5).

**Bottom-up or top-down?**

Within the visual search literature, there has been a lively debate about whether selective attention is mainly stimulus-driven or goal-driven. A number of authors have argued that visual selection is initially stimulus-driven (e.g. Theeuwes, 1991, 1992, 2010; Nothdurft, 2002). Evidence for this view mainly stems from experiments using the irrelevant singleton paradigm, a version of the visual search task. In a typical experiment, observers search for a target that is presented simultaneously with multiple distractors. The target is always a feature singleton, i.e. it differs from the other elements in the display in exactly one feature. On half of all trials, one of the distractors is replaced by another feature singleton that differs from the target. For example, observers might search for a green square among several green circles and one red circle, the singleton distractor (e.g. Theeuwes, 1992). A comparison of response times to the target in trials with a singleton distractor to those without distractor typically shows that responses to the target are slower when the singleton distractor is present than when it is absent. Presumably the salient singleton distractor attracts the observers' attention and thus causes the slowing of response times to the target.

According to a bottom-up view of visual selection, the singleton distractor stands out from the other distractors. As a consequence, this distractor will be selected first and goal-driven selection only occurs on the representation delivered by the bottom-up process, so after bottom-up selection has taken place. That is, top-down selection is contingent on bottom-up selection. In contrast to the view that visual selection is initially stimulus-driven, other authors have argued that attentional capture is contingent on the top-down settings of the observer (e.g. Folk, Remington, & Johnston, 1992; Folk & Remington, 1998). Evidence for this view primarily stems from studies using a cueing version of visual search. For example, Folk et al. (1992) had one group of observers search for an
onset target and another group of observers search for a color singleton target. Prior to the presentation of the target display (150 - 100 ms), an irrelevant location cue was presented at one of the four possible target locations. The cue could either be an onset cue or a color singleton cue. The results demonstrated that performance was worse in the invalidly cued trials but only if the cue matched the target. That is, an irrelevant color cue did not disrupt performance when observers searched for an onset target and an irrelevant onset cue did not disrupt performance when observers searched for a color singleton target. Accordingly, the authors concluded that a salient singleton distractor only captures attention when it matches the observers’ goals. A distractor that is salient, but completely task irrelevant will not capture attention, i.e. stimulus-driven selection is contingent on top-down selection. 

To resolve the question whether selection is mainly bottom-up or top-down, van Zoest, Donk and Theeuwes (2004) studied stimulus-driven and goal-driven saccadic selection over time. They found that time was a major factor determining whether the saccades of their participants were guided by bottom-up or top-down processes (see also van Zoest & Donk, 2005, 2006). According to their view, selection is initially completely stimulus-driven, followed by a phase during which it is purely goal-driven. In contrast to both Theeuwes (1992) and Folk (1992), they do not assume that one mechanism is contingent upon the other. Instead, they claim that bottom-up and top-down processes are independent mechanisms that operate in different time windows.

This timing account of visual selection is able to explain the results that are typically obtained from both irrelevant singleton experiments (e.g. Theeuwes, 1992) and experiments involving cueing (e.g. Folk et al., 1992). In a typical irrelevant singleton experiment, on half of all trials the search display contains two salient elements that differ from all other elements in one, albeit different, feature: the target and the distractor. Early into the trial, when bottom-up processes determine selection, the irrelevant singleton distractor and the target are selected with equal probability. Whenever the distractor is selected, the target can only be selected later when top-down processes determine selection, thus delaying RTs to the target. Thus, average RTs to the target in the presence of an irrelevant singleton distractor are slower than average RTs to the target when this is the only salient element in the search display. In the cueing paradigm used by e.g. Folk et al. (1992) the cue display appears on the screen 150 ms before the display that contains the target. Thus, goal-driven selection of the target possibly takes place only after the effect of cue salience has disappeared. As a consequence, only invalid cues that match the current top-down attentional set (see also section 1.4 of this Introduction) attract attention and lead to prolonged RTs to the target. 

The van Zoest et al. (2004) study emphasizes the relevance of the temporal dimension, something that is supported by recent studies. Hickey, van Zoest and Theeuwes (2010), for example, recorded the electroencephalogram (EEG) to investigate the time course of attentional capture in an irrelevant singleton experiment and used the N2pc component as an indicator of the allocation of attention (cf. Luck & Hillyard, 1994a,b). They separately analyzed those trials in
1.1 Bottom-up: The time course of feature-based salience

which RTs to the target were very slow (the slowest 25% of all trials) and those trials in which target RTs were very fast (fastest 25% of all trials). They assumed that attentional capture by the irrelevant singleton had occurred during the slow RT trials, but not during the fast RT trials. Hickey et al. found that the N2pc to the singleton distractor had a larger amplitude when RTs were slow than when RTs were fast; and an opposite trend for the target-elicited N2pc component. The results support the assumption that shifts of attention that occur immediately after the presentation of a display are primarily directed towards the irrelevant salient singleton distractor. This leads to a large N2pc to the singleton distractor, a small N2pc to the target and slow RTs. Those shifts that occur later on are more often directed towards the target and lead to an opposite pattern of N2pc amplitudes and fast RTs. A similar finding was recently reported by Wykowska and Schubö (2010). In their study, Wykowska and Schubö presented observers with a search display that could contain a target and/or a task-irrelevant singleton among several background elements. This display was masked after a brief presentation duration. Wykowska and Schubö did not find any early EEG differences between trials that contained a target and/or a task-irrelevant singleton. However, they found a more positive N2 component for the target than for the task-irrelevant singleton 230 ms after search display onset, suggesting that goal-driven mechanisms needed some time to develop. Taken together, these studies show that whether attentional selection is predominantly bottom-up or top-down is likely to be dependent on time.

This thesis further investigates the role of time in feature-based visual selection (Chapter 2), top-down selection (Chapter 4, 5), and both (Chapter 3), while taking the factor time into account. In the following sections, I will introduce each of these studies and put them into a broader context than already provided in the individual introductions of each chapter.

1.1 Bottom-up: The time course of feature-based salience

The salience map model by Itti and Koch (Itti et al., 1998; Itti & Koch, 2001) assumes that the visual field location with the highest activation in the salience map is attended first. An inhibition-of-return-like mechanism (IOR, Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985; Klein, 2000) then suppresses the representation of this location in the salience map such that attention can move to the location with the second highest activation after about 30 - 70 ms (Itti, 2000). Thus, the model implies that attention visits locations in the visual field in the order of decreasing salience. However, recent experiments have shown that this might not be the case. Einhäuser, Spain and Perona (2008), for example, presented observers with photographs of objects, scenes and people, and asked them to describe each image with several keywords after the image had been presented for three seconds. They then determined the locations that were fixated by their observers, the locations that were most salient according to the salience map model and the locations of the objects that were used in the image descriptions. Contrary to the salience map model, Einhäuser et al. (2008) found that the locations of previously described objects were a better predictor
of fixations than the salience map. This suggests that the salience of individual features does not influence attentional selection when observers view an image for several seconds. Instead, attention selects those locations that contain meaningful objects.

Whereas Einhäuser et al. (2008) focused on visual selection in a time frame of seconds, van Zoest and Donk (van Zoest & Donk, 2005; Donk & van Zoest, 2008) investigated the development of bottom-up selection during the first hundreds of milliseconds after the onset of a search display in a series of experiments. On each trial, they presented a field of homogeneously oriented lines that included two orientation singletons, one of which was defined as the search target. The other orientation singleton functioned as a distractor, which was either more, less, or equally salient than the target. They asked observers to make a speeded saccade to the target and analyzed the latencies and accuracies of the first saccade after search display onset. Van Zoest and Donk found that the majority of saccades with short latencies ended on the most salient element in the display, irrespective of whether this was the target or the distractor. Saccades with longer latencies, however, were equally likely to end on the target and the distractor. Thus, the relative salience difference between both singletons only affected saccades that were made shortly after the onset of the search display.

This finding was further corroborated by Donk and Soesman (2010), who investigated the time course of salience effects using a probe dot task. They again presented two orientation singletons in a homogenous field of background lines, which was masked after a variable stimulus-onset-asynchrony (SOA). One of the singletons was locally more salient than the other, i.e. it had a bigger orientation difference to the surrounding background lines. This time observers had to indicate the location of a small probe dot within the mask, either at the location of the more salient singleton, the less salient singleton, or at the location of a background element, by pressing a key on the keyboard. They found that responses to the probe dot were faster at the more salient location than at the less salient location, but this was again only the case at the shortest SOA of about 50 ms. This difference disappeared at the longer SOAs (about 160 ms and 480 ms). Responses to both singleton locations always remained faster than responses to background locations. Again, this shows that the relative salience difference between two locations only affects selection briefly after the onset of the search display, whereas both singleton locations continue to affect selection for several hundreds of milliseconds.

Dombrowe, Olivers and Donk (2010b, Chapter 2 of this thesis) investigated the time course of color- and luminance-based salience effects using a similar design as Donk and Soesman (2010). Some authors had suggested that the time course of salience effects may depend on the specific feature dimension within which the contrast occurs (e.g. Parkhurst, Law, & Niebur, 2002; Carmi & Itti, 2006). Therefore, we studied if the time course of salience effects observed in the orientation domain generalizes to other dimensions. We presented two color (Experiment 1) or luminance singletons (Experiment 2) of distinct local salience in a field of homogeneous lines. This display was masked after six different SOAs (30, 60, 120, 240, 480, 960 ms) and observers had to indicate the location
1.2 Bottom-up and top-down: Feature-based selection as a function of time

of a small rotating star (probe) presented either at the previous location of the more salient singleton, the less salient singleton, or one of the background lines. We found that at short SOAs, response times to probes presented at the more salient location were faster than at the less salient location, which were again faster than response times to probes at a background location. At intermediate SOAs, responses to the more salient and the less salient location did not differ, while they were still faster than responses to background locations. Further, the response time benefit set in earlier for the more salient than the less salient location. Thus, the relative salience difference between both feature singletons only affected selection briefly after display onset, which agrees with the findings of earlier studies. Further, the study shows the rise and fall of salience effects. Even though the RT benefit for the less salient location set in later and was smaller than than that for the more salient location, the pattern of results obtained for the less salient singleton was quite similar to the one found for the more salient singleton. The time course of salience effects, i.e., the difference between RTs found to the more relative to the less salient location as a function of SOA, closely resembles the one usually found in spatial cueing studies, with a rapid onset of salience effects that peak around 100 to 200 ms, followed by a decrease (e.g. Nakayama & Mackeben, 1989; Müller & Rabbitt, 1989). Thus, the effects of relative salience in both the color or luminance domain are very similar to the effects of an unexpectedly appearing exogenous cue. This suggests that visual selection may in both cases be determined by the same underlying processes as the onset of a peripheral cue. After all, an onset might just be a local contrast in time.

The most direct explanation of our results is probably provided by a time-based account similar to the ones proposed by Thorpe (2001), VanRullen (2002, 2003) or VanRullen and Koch (2003). VanRullen (2003), for example, argued that an explicit representation of salience in a dedicated map is unnecessary, because salience might be implicitly coded in the relative timing of the first spikes fired. According to this view a more salient object is an object that evokes an earlier neuronal responses and a higher firing rate than a less salient object. Thus, already the first spikes fired in response to distinct objects in the visual field would carry the information which object is more salient, since this object would lead to an earlier firing of the neurons in whose receptive fields it is. As a consequence, the object would be recognized earlier and could thus influence behavior earlier than less salient objects. VanRullen further noted that perceptual tasks such as object categorization can be performed very rapidly, indicating that processing in the visual system is much faster than it would be possible, if a salience map had to be computed. This observation matches with the early salience effects observed by us (Dombrowe et al., 2010b).

1.2 Bottom-up and top-down: Feature-based selection as a function of time

While Chapter 2 only looked at stimulus-driven selection, Chapter 3 investigated the dynamics of both stimulus-driven and goal-driven selection, this time in brain damaged patients with spatial attention deficits.
The interplay between stimulus-driven and goal-driven selection is often assumed to be controlled by a network of brain areas in the frontal and parietal lobes (Mesulam, 1999; Posner & Petersen, 1990; Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Bressler & Menon, 2010). Corbetta and Shulman (2002) identified two sub-networks of this fronto-parietal attention network, the dorsal fronto-parietal network which is responsible for top-down attention, and the ventral fronto-parietal network that directs attention to salient events (i.e. responsible for bottom-up attention). The dorsal network includes (the human homologue of) the frontal eyefield (FEF) and the intraparietal sulcus (IPS) of both hemispheres. The ventral attention network includes the right temporal parietal junction (TPJ) and the right ventral frontal cortex (VFC) of the right hemisphere. It can detect salient events and interrupt activity in the dorsal attentional network. Similar distinctions between sub-networks responsible for bottom-up and top-down processing have been made by other authors. Posner and Petersen (1990), for example, distinguished an anterior and a posterior attention system, which are involved in top-down and bottom-up processing, respectively. Although the existence of the fronto-parietal attention network has been shown to be relevant for the allocation of spatial attention, there is lot of evidence that at least parts of the network are also involved in feature-based selection (e.g. Liu, Slotnick, Serences, & Yantis, 2003; Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007; Greenberg, Esterman, Wilson, Serences, & Yantis, 2010).

Damage to the fronto-parietal attention network often leads to impairments in spatial attention, which are clinically apparent in the symptoms of neglect and extinction (Mesulam, 1981). In particular, lesions within the right IPS, the superior parietal lobule (SPL) and the TPJ have been associated with these types of attention deficits (e.g. Vandenberghe & Gillebert, 2009). Neglect patients often fail to attend to one half of the visual field. Usually this is the contralesional half when the damage is unilateral. For example, in visual search tasks, the patients preferably scan items in the ipsilesional hemi-field and frequently omit items in the contralesional hemi-field (Posner & Petersen, 1990). Patients with extinction are able to report the presence of single stimuli in both halves of the visual field. However, on bilateral stimulation, they fail to report the stimulus in the affected hemi-field.

A lot of studies have investigated the contributions of bottom-up and top-down mechanisms to spatial selection in neglect and extinction (see Bartolomeo & Chokron, 2002, for a review). It appears that it is primarily the bottom-up mechanism of spatial selection that is impaired in the patients, while the top-down mechanism seems largely intact. Làdavas, Carletti, & Gori (e.g. 1994), for example, investigated stimulus-driven and goal-driven spatial selection in neglect patients using uninformative peripheral and informative central cues. They found that the patients did not show a cue validity effect with peripheral uninformative cues, but did so with central informative cues, suggesting that only the bottom-up mechanism was impaired. Dombrowe, Donk, Wright, Oliver and Humphreys (submitted, Chapter 3 of this thesis) studied the contributions of feature-based bottom-up and top-down selection in neglect and extinction.
1.2 Bottom-up and top-down: Feature-based selection as a function of time

patients. Crucially, we took the distinct time courses of these mechanisms into account (cf. Jonides, 1981; Müller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987). This is important, since a number of studies have shown that both neglect and extinction have a temporal dimension (Husain, Shapiro, Martin, & Kennard, 1997; Baylis, Simon, Baylis, & Rorden, 2002; Becchio & Bertone, 2006). For instance, it has been shown that neglect patients have a prolonged attentional blink (Husain et al., 1997) and that extinction patients need a significant temporal lead of a contralesional stimulus in order to perceive it as appearing simultaneously to an ipsilesional stimulus (Baylis et al., 2002).

We used the well-tested experimental design described in section 1.1 that allows the assessment of the allocation of overt attention as a function of time (van Zoest, Donk, & Theeuwes, 2004; van Zoest & Donk, 2005, 2006, 2008, 2010; Donk & van Zoest, 2008). In a typical experiment, participants are asked to make a saccade to one of two orientation singletons embedded in a field of homogeneously oriented lines. The salience of the singletons is usually varied by changing the orientation of the background lines, such that the current target singleton is either more salient, less salient or equally salient as the distractor singleton. In healthy, young participants saccadic target selection typically varies as a function of time. Saccades with short latencies tend to end on the more salient singleton, irrespective whether this is the target or the distractor. With increasing latency, more and more saccades are directed towards the target singleton. Further, as mentioned in section 1.1, the effects of the relative salience difference between the more and the less salient singleton disappear over time, while the influence of goal-driven mechanisms gradually increased.

We found that some of the patients preferentially made saccades into the clinically unaffected hemi-field, i.e. they showed a spatial bias. This is consistent with results obtained by Gainotti, D’Erme and Bartolomeo (1991). Particularly the short latency saccades tended to end in the unaffected hemi-field. With regard to feature-based selection, both the bottom-up and the top-down component were severely impaired in neglect and extinction patients. Bottom-up selection was only impaired when stimuli were presented in the clinically affected hemi-field of the patients. Although the relative salience between the singletons clearly affected early saccades into this hemi-field, it did so to a lesser degree than in the unaffected hemi-field and in comparison to the healthy control group. Further, the salience effect was only present for saccades with very short latencies (earliest 20%). Top-down selection was overall reduced in the patients. The reduction was more pronounced for saccades into the affected hemi-field than for saccades into the unaffected hemi-field. This pattern of results was independent of any spatial attentional biases exhibited by the patients. Thus, the deficits of neglect and extinction patients with regard to top-down selection seem to be dependent on the type of attentional selection. Goal-driven spatial selection seems to be spared, whereas goal-driven feature-based selection seems to be considerably impaired.

To our knowledge, there is only one other study that specifically investigated feature-based top-down selection of stimuli in the ipsilesional hemi-field of pa-
tients with right hemisphere damage. In this study, Snow and Mattingley (2006) used a modified version of the flanker task (cf. Eriksen & Hoffman, 1973; Eriksen & Eriksen, 1974) and presented patients with a colored target letter in the center of the display that was always flanked by two task-irrelevant distractor letters that could be congruent, incongruent or neutral on either the letter or color dimension. The patients had the task to identify either the target color (red or green) or its identity (A or B) and to ignore the other feature dimension as well as the distractors. Responses to the target were given by clicking the left or right mouse button. Snow and Mattingley (2006) found that an ipsilesional presentation of a task-irrelevant distractor that was incongruent within the currently irrelevant feature dimension (e.g., color when participants decided on identity) slowed down the patients’ responses to the targets, whereas a healthy control group could successfully ignore these distractors. On the other hand, the patients showed congruency effects that were comparable those observed in the control group for task-relevant distractor features. The authors conclude that patients with unilateral left neglect cannot inhibit task irrelevant features of stimuli presented in their ipsilesional hemifield. Their results are consistent with ours insofar as both studies found feature-based top-down selection of ipsilesional stimuli to be impaired.

The reduced contributions of stimulus-driven and goal-driven mechanisms to feature-based selection we found in Chapter 2 (Dombrowe et al., submitted) were independent of any spatial biases exhibited by the patients. Informing our patients that the target could be found in the affected hemi-field completely abolished all biases to make saccades preferentially into the unaffected hemi-field. However, this did not increase the availability of salience information or the ability for feature-based selection. This suggests that top-down spatial attention cannot enhance stimulus-driven feature-based processing, neither does it seem to interact with top-down feature-based selection, at least in patients with neglect or extinction, suggesting that spatial and feature-based selection are independent processes.

In a recent review concerning brain regions involved in spatial selection, Vandenberghhe and Gillebert (2009) concluded that the computation of a salience map takes place in the IPS of the right hemisphere, whereas shifts of attention are associated with SPL activity. Activation of the TPJ, the brain area where the major damage of our patients was located, would be primarily associated with the breach of expectancies, such as the occurrence of an infrequent invalid spatial cue. This is in line with theories that see the TPJ as part of a ventral attention network which detects salient events and can interrupt the activity of a dorsal network that primarily controls top-down selection (Corbetta & Shulman, 2002). With regard to our results, this account can explain why our patients were able to direct their spatial attention towards the affected hemi-field when we asked them to do so. Although a TPJ lesion probably contributes to an overall imbalance in the attention network which then leads to a spatial bias towards the unaffected hemi-field, the patients’ dorsal attention network was still functional, allowing them to endogenously reorient spatial attention.
1.3 Top-down: Feature-based working memory effects as a function of time

Many theories of visual attention assume that top-down selection is accomplished by comparing a target template in working memory to the perceptual input (e.g., Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). This mechanism biases selection towards stimuli in the visual field that share features with the target one is currently looking for, irrespective of whether a stimulus actually is the target or not. Thus, sometimes visual attention erroneously selects a non-target that has one or more features in common with the target (cf. Folk et al., 1992). But what if working memory contains a second item that is completely irrelevant for the current task. Can this item also lead to the inadvertent selection of a distractor element? In other words, does an item in working memory automatically result in a selection bias for that item? Some theories, such as Biased Competition (Desimone & Duncan, 1995) state that this should be the case. According to these theories, a memory consists of neural activity corresponding to an object representation, which then automatically results in an advantage of a matching perceived stimulus.

The relationship of working memory and attentional selection also leads to effects in the other direction. Olson, Sledge and Drowos (2008), for example, showed that attended items were sometimes transferred into working memory even when participants had been explicitly told that these items did not have to be memorized. Further, there seems to be a correlation between stimulus-salience and the encoding into working memory. Fine and Minnery (2009), for example, asked their participants to memorize the locations of several target items presented on images of maps. After a short delay, they had the task to indicate where the targets had been located on each map. Fine and Minnery found a negative correlation between recall errors and the salience of the original target locations, suggesting that salience seems to enhance encoding into working memory.

This reciprocal relationship of working memory and attention has led some authors to conclude that both concepts are in fact one and the same. Chun (2011), for example, (see also Chun, Golomb, & Turk Browne, 2011) argues that visual working memory is a form of internally directed attention. He claims that encoding an object and keeping this representation active after the object has disappeared is nothing else than attending to this object in a sustained manner. Similar to FIT, attention here serves as a means to bind the individual features of an object. Maintaining this binding in the absence of the represented object is, from this point of view, both sustained attention to this object and storing the object in working memory.

Dombrowe, Olivers and Donk (2010a, Chapter 4 of this thesis) noted that previous studies obtained inconsistent results regarding the issue whether task-irrelevant accessory memory items automatically attract attention. Some studies found attentional capture by task-irrelevant items held in working memory (e.g. Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Heinke, 2006), whereas other studies did not find such an effect (e.g. Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Woodman &
These studies even used very similar experimental designs, which makes the diverging results quite surprising. In these experiments, participants first memorized a simple color or shape and then looked for an unrelated target in a visual search display. They then completed a memory test. The authors of these studies usually compared a condition where the memory item reappeared as a distractor in the search display to a condition where it did not reappear. A slowing of RTs to the target in the distractor present condition relative to the distractor absent condition would usually be interpreted as an indication that the reappearing memory item in the search display had captured the participants’ attention. We (Dombrowe et al., 2010a) noticed that despite the design similarities, all previous studies had used very different SOAs between the memory item and the search display, allowing for the possibility that time plays an important role again. Further, Olivers, Meyer and Theeuwes (2006) had found attentional capture by a task-irrelevant working memory item only when this item was visually represented in working memory, while an item that could be verbalized did not capture attention. We then varied the SOA between the memory item and the search display for more verbal, as well as for more visual working memory items. We found that the effects of more verbal working memory content on visual attention decreased with increasing SOA, while the effects of more visual working memory content were more sustained. Thus, the discrepancies between previous results seem to be at least partially due to the timing used in these studies.

1.4 Top-down: The time course of switching attentional sets for features

Top-down selection is goal-driven. As discussed in the previous section a goal can, for example, be represented in the form of a target template in working memory that specifies the features of an object one is currently looking for. Top-down selection is often thought to be accomplished by comparing this template to the perceptual input (see also section 1.3). However, working memory might contain more items than just the target template. It has been shown that accessory items in working memory compete for the status of attentional set, that can only contain one item at a time (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2009; Olivers & Eimer, 2010; Olivers, Peters, Houtkamp, & Roelfsema, 2011). As mentioned early in this Introduction, this set not only guides selection towards the target one is currently looking for, but it might also lead to the involuntary selection of a distractor item that shares a target feature (i.e. contingent capture; Folk et al., 1992; Folk & Remington, 1998).

People might have more than one goal. They might, for instance, search for two targets of different colors. In this case, they would be looking for two features. This would presumably require two attentional sets, one for each color. It has been shown that searching for more than one feature is typically associated with a cost, in particular when the features are of the same dimension (e.g. two colors). This is true whenever people search for one object with two features (Wolfe, Stewart, Friedmanhill, Yu, Shorter, & Cave, 1990) or two objects with one feature each (Moore & Osman, 1993). Is there also a cost when people...
1.4 Top-down: The time course of switching attentional sets for features

switch from one attentional set to another?

This question has been studied only occasionally (Vickery, King, & Jiang, 2005; Wolfe, 2004; Rushworth, Passingham, & Nobre, 2005). However, switching the more broader task set has been studied quite extensively (see e.g. Monsell, 2003). Task switching not only comprises a switch in attentional set, but also in stimulus-response mappings (Rushworth, Paus, & Sipila, 2001). Task switching was first explored by Jersild (1927), who asked participants to apply arithmetic operations (addition and subtraction) to lists of numbers. In one condition, participants had to apply only one of the operations (no task switch necessary), in the other condition they were asked to alternate between addition and subtraction (task switch required). Jersild (1927) found that it took his participants longer to complete the condition that required a task switch than the condition that did not. He concluded that switching between tasks is associated with a cost.

In Chapter 5 of this thesis (Dombrowe, Donk, & Olivers, in press), we presented our participants with a display consisting of four circles of different colors on the left side of fixation and another display with four circles on the right side. Each side contained a target circle. Participants had the task to make a saccade to the target circle on one side, followed by a saccade to the target circle on the other side. They were asked to try to be as fast as possible. The displays were presented sequentially, with the second display appearing and the first display disappearing as soon as participants looked at the first target, to prevent that the saccade to the second target could be pre-programmed. Both targets were either of the same color (no-switch condition) or of different colors (switch condition). By always presenting the target displays in the same order, and consistently tying them screen locations, we sought to enable observers to simultaneously maintain both attentional sets in working memory (cf. Adamo, Pun, Pratt, & Ferber, 2008; Moore & Weissman, 2010, 2011) and thus minimize or even abolish switch costs. If performance suffers even under these optimal circumstances, we can conclude that switching attentional sets is associated with a cost.

Our results show that saccades were less accurate and slower in the switch condition than in the no-switch condition. This indicates that switching attentional sets is indeed associated with a cost. Further, whenever one of the distractors had the color linked to the first attentional set, a substantial proportion of saccades ended on this distractor instead of on the target. An analysis of the time course revealed that this distractor preference changed to a target preference about 250 - 300 ms after stimulus onset, suggesting that this is the time required to switch attentional sets.

Task switch costs decrease with increasing time available to prepare the switch. However, they do not seem to disappear entirely. Rogers and Monsell (1995), for example, created predictable task sequences for their participants. Further, they increased the available preparation time up to 1200 ms, an interval that should allow for a complete reconfiguration from one task set to another. However, Rogers and Monsell still observed switch costs of about 200 - 300 ms, which they termed residual switch costs. The fact that these residual costs are very simi-
lar to the attentional set switch costs found by Vickery et al. (2005); Wolfe (2004); Rushworth et al. (2005) and again by us (Dombrowe et al., in press), suggests that these costs might be identical. That is, the residual switch costs might reflect the 200-300 ms it takes under optimal circumstances to switch from one attentional set to another.

1.5 Conclusion

All studies collected in the present thesis support the assumption that the factor time plays an important role in visual selection. This is true for both stimulus-driven and goal-driven feature-based selection (Chapters 2 and 3), including changes in attentional set (Chapter 5), and for the influence of working memory content on selection (Chapter 4). Previous conclusions on whether selection is mainly bottom-up or top-down driven, or whether memory does or does not affect attention, have often been based on measurements at single moments in time. However, these provide only a snapshot of what are dynamic, evolving and interacting processes.
Salient objects in the visual field attract our attention. Recent work in the orientation domain has shown that the effects of the relative salience of two singleton elements on covert visual attention disappear over time. The present study aims to investigate how salience derived from color and luminance differences affects covert selection. In two experiments, observers indicated the location of a probe which was presented at different stimulus-onset-asynchronies after the presentation of a singleton display containing a homogenous array of oriented lines and two distinct color singletons (Experiment 1) or luminance singletons (Experiment 2). The results show that relative singleton salience from luminance and color differences, just as from orientation differences, affects covert visual attention in a brief time span after stimulus onset. The mere presence of an object, however, can affect covert attention for a longer time span regardless of salience.

The time course of color- and luminance-based salience effects.
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2 The time course of salience effects

2.1 Introduction

A distinct object in the visual field tends to attract our attention (Nothdurft, 2002; Theeuwes, 1992; Wolfe & Horowitz, 2004). One possibility to account for this effect is to assume that the visual system contains a salience map (Itti, 2000; Itti & Koch, 2001; Koch & Ullman, 1985). The salience map is a combined topographical representation of the relative conspicuity of locations in the visual field. It is computed from several separate feature conspicuity maps in a parallel fashion (Itti, Koch, & Niebur, 1998). Attention then visits the locations in the visual field in order of decreasing salience-related activity.

An important question is how salience effects develop over time. That is, how do they emerge, do they change as a function of time and if yes, how? According to the salience map model, the effects of salience indeed change. Within this model, the active locations representing salient objects are eventually inactivated by a mechanism denoted as inhibition of return (IOR, Posner & Cohen, 1984; Posner, Rafal, Choate, & Vaughan, 1985; Klein, 2000). This is assumed to be necessary to allow shifts of attention. For example, within the Itti, Koch and Niebur (1998) model implementation, the activity at visited locations is set to zero, so that the next object can be selected.

Recent work by Donk and colleagues has confirmed that the effect of salience indeed changes across time, but their finding suggest a different mechanism. In one study by Donk and van Zoest (2008), observers were instructed to make a rapid eye movement to the more salient of two line segments, as defined by the difference in orientation relative to a background of homogeneously oriented line segments. Even though only the relative salience of the two objects was relevant to the task, its effect decreased considerably as saccade latency increased. At short latencies eye movements were more likely to go to the more salient object, whereas long-latency eye movements were equally likely to be directed to the more and the less salient line segment. Both were more likely to be selected than the background. In other words, an initial salience bias was replaced by a general tendency to select any outstanding object, irrespective of its salience value. Donk and Soesman (2010) further investigated the time course of salience effects. In their study salience was completely irrelevant to the task. Again the stimulus consisted of two orientation-defined elements embedded in a field of homogeneously oriented background lines. Now the task was to respond to a colored probe presented at three different stimulus-onset-asynchronies (SOAs) after the orientation display. The probe could appear at either the more salient location, the less salient location, or a background location. At the shortest SOA (42 ms), Donk and Soesman found a relative RT benefit for the more salient location over the less salient location, but this effect was again transient: at longer SOAs (158 ms and 483 ms), the difference between the more and the less salient location disappeared, while both locations retained their advantage over the background locations. Thus, relative salience seems to have an initial expediting effect on segmenting objects from their background, but once segmented, the salience difference between objects no longer affects selection (see also Einhäuser, Spain, & Perona, 2008; Itti, 2005, for similar suggestions). Furthermore,
these representations do not appear to be suppressed towards or beyond baseline levels (as would be indicative of classic IOR).

Instead, Donk and colleagues (van Zoest et al., 2004; van Zoest & Donk, 2005, 2006, 2008; Donk & van Zoest, 2008) proposed on the basis of these and other studies that a salient object differs from a less salient object not because it generates a different amount of activity in the salience map, but because it generates activity at an earlier point in time (see also: Thorpe, 2001; VanRullen, 2002, 2003). As a consequence, visual selection is predicted to be only affected by the relative salience of objects as long as there is differential activity in the salience map. After some time has elapsed, both a salient and a less salient object are equally likely to attract attention since both are equally strongly represented in the system. Salience is thus perceived as an emergent property of the temporal order, rather than the level, in which objects generate activity in the salience map.

However, the conclusions of Donk and Soesman (2010) were based on a limited set of data points. Moreover, the implications of their results are strongly limited by the fact that salience was defined in the orientation domain only. There are several studies suggesting that the time course of salience may depend on the specific visual dimension at which the contrast occurs. For example, a study by Parkhurst, Law and Niebur (2002) compared the influence of individual feature dimensions on eye movements and found that color and luminance differences had a stronger influence on fixation locations than orientation differences (at least for images that were not dominated by straight lines). Differences among feature dimensions have also been reported by others (e.g. Engmann, ‘t Hart, Sieren, Onat, König, & Einhäuser, 2009; Carmi & Itti, 2006). For example, using short video clips, Carmi and Itti (2006) found that both color and intensity contrast contributed more to stimulus-driven overt selection than orientation contrast, but less so than motion contrast. Moreover, an analysis of the time course revealed that the influence of color contrast decreased over the first saccades, while the influence of luminance contrast increased during that time. Taken together, these studies suggest that whether or not salience effects are transient may well depend on the specific dimension tested. It is therefore important to test whether the transience found for orientation generalize to other dimensions. This was done for color (Experiment 1) and luminance (Experiment 2).

In both experiments, observers were instructed to detect and manually respond to a probe, which was defined by motion. As in Donk and Soesman (2010), the probe display was preceded by a display consisting of mainly background elements at various SOAs. This display also contained two singleton objects, one more salient than the other (defined by a color or luminance difference to the background). The subsequent probe could appear at either one of these locations, or at a background location. To allow a closer examination of the time course of relative salience effects, we now used six different stimulus durations ranging from 30 ms to 960 ms.

We predicted that if the transience of relative salience is not specific to orientation, it should generalize to color and luminance. Moreover, the more precise time course allowed us to assess whether the two differential salience representations indeed have an asynchronous onset, but then merge into the same level
of activation, as predicted by the timing account explained above.

General Method

Participants

In total 22 students of the Vrije Universiteit Amsterdam participated for either course credit or 7 euro. Of these, 8 students participated in Experiment 1 and 14 students in Experiment 2. They all reported having normal or corrected-to-normal visual acuity. None of the participants reported to be color blind.

Apparatus

An HP Compaq d530 CMT Pentium IV computer running E-Prime (Psychology software tools, 2003) generated the stimuli on a color calibrated iiyama Vision Master Pro SVGA 120-Hz screen and acquired the necessary response data through the standard keyboard. Display resolution was $1024 \times 768$ pixels. The experiment was run in a dimly-lit room at a viewing distance of about 80 cm.

Stimuli

We presented a singleton display followed by a probe display. The singleton display consisted of a field of oriented lines (background) and two singleton elements differing from the background elements either in terms of color (Experiment 1) or luminance (Experiment 2). One of the singletons was always more salient (i.e. it was highly distinct from the background elements), the other singleton was always less salient (i.e. it was similar to the background elements). All elements, including the singletons, were 0.8 degrees long, 0.2 degrees wide and always had an orientation of 45 degrees clockwise from the vertical. They were arranged in a $21 \times 29$ (height $\times$ width) rectangular matrix, with the central element (at position row=11/column=15) omitted and replaced by a fixation cross. The singletons were presented on the corners of an imaginary square around the fixation cross (at positions row=7/column=11, row=7/column=19, row=14/column=11 and row=14/column=19 of the matrix). These locations all had a distance of 4.3 degrees from the center of the screen. After a variable presentation duration, the singleton display was replaced by a probe display containing multiple asterisk-like elements. Each ‘asterisk’ consisted of six lines of the same length and width with different color (Experiment 1) or luminance values (Experiment 2). One ‘asterisk’ rotated clockwise at about 5 turns per second (probe). The probe was presented at one of the four possible singleton locations. All stimuli were presented on a black background ($0 \text{ cd/m}^2$). The fixation cross was gray (CIE $x$, $y$ coordinates of 0.303; 0.344). Figure 3.1 depicts both the singleton display and the probe display.

In Experiment 1, we used two different color singletons, i.e. red (CIE $x$, $y$ coordinates of 0.619; 0.342) and green (CIE $x$, $y$ coordinates of 0.296; 0.609), and two different background colors, i.e. orange (CIE $x$, $y$ coordinates of 0.428; 0.348) and
dark green (CIE x, y coordinates of 0.244; 0.413). We created two singleton displays: a more salient red singleton and a less salient green singleton among dark green background elements and a more salient green singleton and a less salient red singleton among orange background elements. We used the colors of both sets and two additional grays (CIE x, y coordinates of 0.303; 0.346 and 0.303; 0.344) for the mask elements. All colors were equiluminant (about 12 cd/m²).

In Experiment 2, we used two singletons with different luminance values. The more salient singleton had a luminance of 50.56 cd/m², the less salient singleton a luminance of 30.29 cd/m², and the background elements a luminance of 8.9 cd/m². Thus, the more salient element was the brightest element in the display, whereas the background elements were the least bright. We used three additional luminance values for the mask elements in the probe display; 17.25 cd/m², 70.67 cd/m² and 16.98 cd/m².

**Procedure and Design**

Each trial started with the presentation of a fixation cross. After one second the singleton display appeared on the screen for either 30 ms, 60 ms, 120 ms, 240 ms, 480 ms or 960 ms (*presentation duration*). Participants were instructed to ignore this display and keep looking at the fixation cross. The display was then masked by a probe display and a short simultaneous tone (100 ms) was presented, indicating that observers were to report the location of the probe. The singleton locations were not predictive with respect to the probe locations, i.e. on half of the trials the probe was presented at a singleton location (with a quarter of trials on the more salient, the other quarter on the less salient), on the other half it was presented at a background location. Participants were asked to indicate the position of the probe by pressing the ’a’, ’z’, ’m’ or ’k’ key for ’up left’, ’down left’, ’up right’ or ’down right’, respectively. A new trial started immediately after the participant’s response. Participants were instructed to remain fixated throughout the whole experiment. Participants first completed 48 practice trials.

Figure 2.1: Schematic depiction of the stimuli used in Experiments 1 and 2.
The time course of salience effects

There were four possible probe locations, two singleton locations and two background locations. Thus, there were 144 trials (24 trials per cell) for each singleton location and 288 trials (48 trials per cell) for the background locations. Participants were asked to respond as fast and as accurately as possible. We used a within-subject design for each experiment.

2.2 Experiment 1

The aim of Experiment 1 was to investigate the temporal dynamics of salience derived from color differences using a probe-RT task. We created two different sets of colors. One of the singletons was always red and one was always green. The color of the background lines differed such that the green singleton was more salient against an orange background and the red singleton was more salient against a green background. Presentation duration was varied across a broad range of values ranging from 30 ms to 960 ms. We used a motion-defined probe in order to preclude any effects of a top-down attentional set for color (e.g. Folk, Remington, & Johnston, 1992). Observers had to locate the rotating mask element.

Results and Discussion

We restricted our RT analysis to trials on which participants had correctly indicated the position of the rotating probe. Reaction times of 2.5 standard deviations above or below the arithmetic mean were excluded for each participant. This resulted in the loss of 5.2% of all trials of Experiment 1. Figure 2.2 shows the mean of the remaining RTs for each of the probe locations (more salient, less salient, and background) as a function of presentation duration (30 ms, 60 ms, 120 ms, 240 ms, 480 ms, 960 ms). An overall ANOVA with the same factors revealed a main effect of probe location \( F(2, 14) = 19.567, p < 0.001 \) and an interaction of probe location with presentation duration \( F(10, 70) = 5.346, p < 0.01 \).

Participants reacted overall faster to probes presented at more salient locations \( M=537 \) ms than to those at less salient locations \( M=541 \) ms or at background locations \( M=546 \) ms. To further assess the interaction we performed separate one-way ANOVAs for each presentation duration. This resulted in significant effects of salience for the durations of 60 ms \( F(2, 14) = 12.968, p = 0.001 \) and 120 ms \( F(2, 14) = 14.958, p < 0.001 \), and a marginally significant effect of salience for the duration of 480 ms \( F(2, 14) = 2.985, p = 0.083 \). For each duration (including 480 ms) we then performed all three post-hoc pairwise comparisons, which were bonferroni-corrected. This revealed significant differences between the more salient and the less salient locations at a presentation duration of 60 ms \( t(7) = 4.316, p < 0.01 \), the more salient and the background locations at presentation durations of 60 ms, 120 ms and 480 ms (60 ms: \( t(7) = 4.220, p < 0.01 \); 120 ms: \( t(7) = 3.936, p < 0.01 \); 480 ms: \( t(7) = 4.365, p < 0.01 \)), and the less salient and the background locations at a presentation duration of 120 ms \( t(7) = 5.257, p < 0.01 \). Participants made relatively few errors at indicating the location of the rotating probe \( M=5.4\% \). A within-subjects ANOVA with probe location (more salient,
2.3 Experiment 2

In Experiment 2 we investigated how salience defined by luminance contrast dynamically affects visual selection. To this end, we presented observers with displays consisting of a homogenous field of gray oriented lines and two different luminance singletons.

less salient, background) and presentation duration (30 ms, 60 ms, 120 ms, 240 ms, 480 ms, 960 ms) did not reveal any effects.

We additionally checked if the results for the two displays differed from each other with an ANOVA with display as additional factor. There was neither a main effect of display \([F(1,7)=2.161, p > 0.1]\), nor did any interactions with this factor reach significance.

Our results show that the time course of salience from color overall resembles the time course of salience from orientation as described by Donk and Soesman (2010). For both orientation and color, salience effects occurred earlier in time at the more salient location than at the less salient location. Then, salience differences between both singleton locations disappeared while both singleton locations still differed from background locations.

Figure 2.2: Mean RTs for each of the probe locations as a function of presentation duration in Experiment 1. Asterisks denote a significant main effect of the one-way ANOVA comparing the three probe locations at one presentation duration.
The time course of salience effects

Results and Discussion

Figure 2.3 shows the mean RTs for each probe location as a function of presentation duration. The data were analyzed in the same way as in Experiment 1. Removing RTs beyond 2.5 standard deviations from the mean resulted in a loss of 2.7% of all trials. The ANOVA of the individual mean RTs with probe location (more salient, less salient, background) and presentation duration (30 ms, 60 ms, 120 ms, 240 ms, 480 ms, 960 ms) as factors revealed a main effect of probe location \[F(2, 26)=12.864, \ p < 0.001\] and an interaction of probe location and presentation duration \[F(10, 130)=3.940, \ p < 0.01\]. Participants reacted faster to probes presented at more salient locations (M=539 ms) than to those presented at less salient locations (M=548 ms) or background locations (M=553 ms). Separate one-way ANOVAs for each presentation duration revealed significant effects of salience for the durations of 60 ms \[F(2, 26)=4.233, \ p < 0.05\], 120 ms \[F(2, 26)=22.169, \ p < 0.001\] and 240 ms \[F(2, 26)=4.923, \ p < 0.05\]. The pairwise comparisons revealed significant differences between the more salient locations and the less salient locations at a presentation duration of 120 ms \(t(13)=3.486, \ p < 0.01\), between the less salient locations and the background locations at presentation durations of 120 ms and 240 ms (120 ms: \(t(13)=3.444, \ p < 0.01\); 240 ms: \(t(13)=3.139, \ p < 0.01\)) and between the more salient locations
2.4 General Discussion

and the background locations at presentation durations of 60 ms and 120 ms (60 ms: t(13)=2.901, p = 0.014; 120 ms: t(13)=6.199, p < 0.001). At a presentation duration of 60 ms, the comparison between the more salient locations and the less salient locations and the comparison between the more salient locations and the background locations at a presentation duration of 240 ms just failed to reach significance under the bonferroni corrections (60 ms, more salient vs. less salient: t(13)=2.543, p = 0.025; 240 ms, more salient vs. background: t(13)=2.653, p = 0.02).

Participants only made few errors in indicating the position of the rotating probe (M=4.1%). An ANOVA with probe location and presentation duration as factors revealed a main effect of probe location [F(2, 26)=6.666, p < 0.05]. Observers made fewer errors when probes were presented at more salient locations (M=3.0%) than at other locations. Error percentages were similar for less salient and background locations (less salient: M=5.0%, background: M=4.1%).

Our results show that the time course of visual salience from luminance contrast is very similar to that from orientation and color contrast. Since we used six presentation durations between 30 ms and 960 ms we were able to describe the time course of visual salience in more detail than Donk and Soesman (2010). Apparently, salience from luminance contrast only emerges after 30 ms. Then, salience representations are graded, in that a more salient location can be differentiated from a less salient location in the salience map. However, this difference soon vanishes (at presentation durations longer than 120 ms), such that both singleton locations are represented as equally salient. About 480 ms after stimulus onset any salience representations regarding the four probe locations seemed just to have disappeared.

2.4 General Discussion

The present study aimed to examine the time course of relative color- and luminance-based salience effects. We distinguish relative salience, the difference in salience between two locations that stand out from their surroundings from the mere presence of salience, i.e. the fact that these locations stand out from their surroundings. Whether luminance- or color-defined, and whether more or less salient, the presence of a salient object transiently improved probe detection, with performance peaking around 60 ms to 120 ms, after which RTs slowed again. Overall, this time course resembles the time course of spatial cueing effects as reported by Nakayama and Mackeben (1989) and Müller and Rabbitt (1989). Measuring accuracy, they found optimal performance for a latency of around 100 ms between a salient onset cue and a visual search target, after which accuracy declined again. They suggested that the cue attracted attention, but only transiently. Note that in the current experiments too, overall performance declined again, with RTs at the longest SOA (960 ms) being no different from the background baseline. This overall transience may indeed reflect a passive decay of attention. Alternatively, the disappearance of overall singleton presence effects could be due to top-down influences, possibly reflecting the participants’ knowledge that singleton locations were uninformative about the
location of the upcoming probe. This presentation duration might have been long enough for the participants to ignore the singleton display and indicate the location of the probe dot irrespective of the preceding singleton locations (including background locations).

The most important result was that for both color and luminance, probe RTs were differentially affected by relative singleton salience only briefly after the presentation of the singleton display. Probe RTs to the more salient location were faster than probe RTs to the less salient location or background locations. This RT benefit appeared earlier at the salient location than at the less salient location. However, the different salience effects at the more salient location and at the less salient location were only transiently present: the difference between RTs to probes presented at more salient and less salient locations disappeared after a presentation duration of 60 ms for color and after a presentation duration of 120 ms for luminance. RTs to singleton locations remained faster than to background locations beyond these 60-120 ms, up to about 500 ms when it has disappeared, indicating more sustained effects of object presence than of relative object salience (in line with Einhäuser et al., 2008; Itti, 2005). Eventually, at the longest presentation duration, probe RT was unaffected by either singleton salience or singleton presence.

The time courses of color- and luminance-based salience effects were very similar to the ones found by Donk and Soesman (2010) in the orientation domain. This suggests that the time course of salience effects does not depend on the specific feature dimension. Our results differ from those of the eye movement studies of Parkhurst et al. (2002) or Carmi and Itti (2006), for example, in that they did find feature-based differences. However, one has to keep in mind that these studies investigated the allocation of overt attention over the course of several eye movements. Thus, it is possible that different feature dimensions only differentially influence overt selection over the course of several saccades, but not covert selection up to the first saccade.

The sustained benefits for more or less salient objects relative to the background is difficult to explain by a classic IOR mechanism (Posner & Cohen, 1984). Furthermore, an active bias away from the most salient item would predict performance for this location to deteriorate back towards background performance, before the next salient item could be prioritized. Neither appeared to be the case, except the return to baseline levels at the longest presentation duration, but which occurred for both items.

The results obtained in the present study can be more directly explained with a dynamic salience account as proposed by Donk and Soesman (see also Donk & van Zoest, 2008) stating that a more salient location relative to a less salient one does not elicit more activation in the salience map (which would then need to be suppressed), but merely elicits activation at an earlier point in time (see e.g. VanRullen, 2003; Thorpe, 2001, for related proposals). Accordingly, salience can be regarded as an emergent property of the time required for individual locations to maximally activate the corresponding locations in the salience map. This means that the most salient location would be represented first and solely (the more salient location in our experiments). After some time, the second-to-
most salient location (the less salient location in our experiment) would also be represented, albeit initially with a lower activation. With a longer stimulus duration, as both items become segmented from the background, activity becomes more and more similar until they are equally active. This way, the time course of visual salience emerges naturally from object segmentation mechanisms.
Feature-based selection in patients with spatial attention deficits

When people search a display, fast saccades tend to be predominantly stimulus-driven, whereas slower saccades become increasingly goal-driven. Here we use this pattern to assess whether patients with lateralized spatial attention deficits such as neglect and extinction are impaired in stimulus-driven processing, goal-driven processing, or both, when selecting feature-defined targets. A group of patients and a group of healthy, age-matched controls were asked to make a saccade to one of two differently oriented lines presented amongst homogeneous background lines. We systematically varied the salience of these lines by changing the orientation of the background elements. Using a multinomial model, we decomposed the individual speed-accuracy functions into the underlying stimulus-driven and goal-driven components. Stimulus-driven processing of stimuli in the more affected hemi-field of the patients was initially present, but was reduced compared to the less affected hemi-field and to controls. Goal-driven processing tended to be overall reduced in the patients. This pattern of results did not depend on an overall spatial bias towards the less affected hemi-field. Our results show that lateralized spatial attention deficits affect both stimulus-driven and goal-driven feature-based selection.

Dombrowe, I., Donk, M., Wright, H., Olivers, C.N.L., & Humphreys, G.W (in revision).
3.1 Introduction

Whenever we search for an object in a visual scene, our eye movements are thought to be guided by two processes. A top-down or goal-driven process which biases attentional selection towards stimuli that match the features of the object we are currently looking for, and a bottom-up or stimulus-driven process biasing selection towards features that are salient relative to their surroundings (Treisman & Gelade, 1980; Duncan & Humphreys, 1989; Wolfe, 1994; Bundesen, 1990; Desimone & Duncan, 1995; Koch & Ullman, 1985; Itti & Koch, 2001).

The interplay of goal-driven and stimulus-driven processes is thought to be controlled by a network of several interconnected brain areas in the frontal and parietal lobes (Mesulam, 1999; Posner & Petersen, 1990; Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Bressler & Menon, 2010). Damage to this network leads to deficits in visual selection that are clinically apparent in the symptoms of neglect and extinction (Mesulam, 1981). In particular, lesions of the posterior parietal lobe and the temporo-parietal junction (TPJ) have been associated with lateralized spatial attention deficits such as neglect and extinction (Mort, Malhotra, Mannan, Rorden, Pambakian, Kennard, & Husain, 2003; Karnath, Himmelbach, & Küker, 2003; Shomstein, Lee, & Behrmann, 2010; Mavritsaki, Allen, & Humphreys, 2010). Patients with neglect often fail to attend to one half of the visual field - the contralesional half when the damage is unilateral. For example, in visual search tasks, these patients preferably scan items in the ipsilesional hemi-field, frequently omitting items in the contralesional hemi-field (Posner & Petersen, 1990). Concurrent eye movement monitoring usually shows that the first eye movements are preferably directed towards the ipsilesional part of the visual field (Gainotti, D’Erme, & Bartolomeo, 1991). In addition, saccades into the contralesional hemi-field tend to have longer latencies than saccades into the ipsilesional hemi-field (Girotti, Casazza, Musicco, & Avanzini, 1983) and often undershoot contralesionally presented targets (Ishiai, Furukawa, & Tsukagoshi, 1987). Patients with extinction can successfully report the presence of single stimuli in both halves of the visual field. However, on bilateral stimulation, they fail to report the stimulus in the affected hemi-field. This deficit is maximal when both stimuli are presented simultaneously and decreases when an asynchrony is introduced (di Pellegrino, Basso, & Frassinetti, 1998; Baylis, Simon, Baylis, & Rorden, 2002; Mavritsaki, Heinke, Deco, & Humphreys, 2009).

An important question is whether it is the top-down or the bottom-up component of visual attention that is affected in neglect and extinction patients, or both. There has been extensive research on the relative contributions of these processes in these patient groups (see Bartolomeo & Chokron, 2002, for a review), but most of this evidence comes from spatial cueing studies (Posner, 1980). For example, Ládavas, Carletti and Gori (1994) have used peripheral uninformative cues as well as central informative cues to investigate stimulus-driven orienting and goal-driven orienting, respectively. Their patients did not show a cue validity effect with peripheral uninformative cues, but did so with central informative cues for contralesional targets. Ládavas et al. (1994) concluded that their patients were impaired in stimulus-driven orienting towards the affected
hemi-field, whereas top-down orienting seemed to be intact. The same conclusion was reached by Smania, Martini, Gambina, Tomelleri, Palamara, Natale, & Marzi (1998) who presented single targets at different eccentricities in the affected or unaffected hemi-field of neglect and extinction patients. They found that patients were less accurate and slower in reacting to targets in the affected hemi-field than in the unaffected hemi-field when the target randomly appeared on either side. When target sides were blocked, the performance of their patients improved, suggesting that top-down orienting to the affected hemi-field can compensate for the deficit in stimulus-driven orienting.

In the present study, we investigate feature-based attention. The method that is most often employed to study feature-based selection is visual search. Behrmann, Ebert and Black (2004), for example, tested a large number of patients with diverse brain lesions on feature and conjunction search, assuming that feature search would primarily rely on bottom-up processes, whereas conjunction search would be mainly based on top-down processes (cf: Treisman & Gelade, 1980). They found that brain damaged patients in general were impaired in both types of search, with the deficits being especially pronounced in neglect patients. Recently, Bays, Singh-Curry, Gorgoraptis, Driver and Husain (2010) tracked the eye movements of patients with parietal lesions searching for a target that was isoluminant with the background and hence relatively difficult to detect, which presumably made search more goal-driven. On some trials however, they presented a highly salient probe instead of the target. Their patients were not only impaired in the goal-driven search task, but also looked at the salient probe less often than healthy controls. They concluded that both top-down and bottom-up feature-based processing were damaged to the same degree.

Here we use a visual search task to investigate the relative contribution of top-down and bottom-up components on feature based selection, as measured through saccadic eye movements. An important extension to previous work is that we assess the relative contribution of both components as a function of time. Although neglect and extinction are often viewed as spatial deficits, both syndromes have a clear temporal dimension (Husain, Shapiro, Martin, & Kennard, 1997; Baylis, Simon, Baylis, & Rorden, 2002; Becchio & Bertone, 2006). However, the temporal aspects of selection in patients with neglect have only been investigated in spatial cueing studies (e.g. Posner, Cohen, & Rafal, 1982; Posner, Walker, Friedrich, & Rafal, 1984; D’Erme, Robertson, Bartolomeo, Daniele, & Gainotti, 1992; Bartolomeo, Siéroff, Dechaix, & Chokron, 2001). Little is known about the temporal dynamics of feature-based selection. However, there is a lot of evidence that bottom-up and top-down selection have different time courses (Jonides, 1981; Müller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987; van Zoest, Donk, & Theeuwes, 2004). We use an experimental design that assesses the allocation of overt visual selection as a function of time (here saccadic latency). This design has been successfully applied to young and healthy populations (van Zoest, Donk, & Theeuwes, 2004; van Zoest & Donk, 2005, 2006, 2008, 2010; Donk & van Zoest, 2008). In the typical experiment, participants are asked to make a direct eye movement to one of two orientation singletons (i.e. target and distractor) both of which are embed-
ded in a homogenous field of oriented lines. Target identity (e.g. a horizontal line) stays constant for at least one block of trials, while target salience (more salient, equally salient or less salient than the distractor) is varied. In healthy, young participants, target selection typically varies with saccadic latency. Saccades with a short latency tend to be directed to the more salient singleton in the search display, irrespective of whether this is the target or distractor. With increasing saccadic latencies more and more eye movements are directed to the target singleton and the contribution of salience is reduced (indexed by saccades to the singleton distractor).

In two experiments, we presented the same task to a group of patients with lateralized spatial attention deficits resulting from inferior parietal lesions (including the TPJ for all but one patient). Figure 3.1 shows some example displays, in which the participant’s task was to make a saccade to the vertical line, while the horizontal line was the distractor (it could be the other way around in other sessions). The orientation of the background lines was used to systematically vary the relative salience of the target and distractor, such that the target was the more salient one (Figure 1a), the less salient one (Figure 1b), or as salient as the distractor (Figure 1c). The target and distractor could both appear in the same hemifield, or in different hemifields. Of most interest was the case when they both appeared in the same hemifield, because we were interested in the relative contributions of bottom-up (stimulus-driven) and top-down (goal-driven) processes to saccadic visual selection in time and how these contributions were different in their affected hemi-field, as compared to their relatively unaffected hemi-field (as well as compared to age-matched healthy control participants). More specifically, do spatial attention deficts lead to deficits in stimulus-driven selection, goal-driven selection, or both? To answer these questions, we fitted a multinomial model which allows us to decompose the speed-accuracy functions resulting from the search task into the underlying top-down and bottom-up biases towards the target element and the most salient element, respectively. To

![Figure 3.1: Examples of displays with a vertical target and a horizontal distractor in the same hemi-field. Arrows depict the saccades to the target. Salience levels from left to right: (A) Target more salient than the distractor, (B) Target less salient than the distractor, (C) Target and Distractor equally salient. All conditions were presented mixed within a block.](image-url)
foreshadow, we found deficits in top-down as well as bottom-up processing of stimuli in the more affected hemi-field. Top-down processing in the less affected hemi-field was also reduced, but less so than in the more affected hemi-field. Bottom-up processing in the less affected hemi-field was intact.

3.2 Experiment 1

Participants

Six patients with lateralized spatial attention deficits participated in the experiment. Five had lesions that included the TPJ region. The lesion of the sixth patient, MH, was somewhat more superior, centralized around the left IPS, but it nevertheless bordered the TPJ area (see Table 3.1 for patient details, Figure 3.2 shows the lesion sites for each patient). The figure depicts T1 structural scans (taken at 3T, with a 1mm isotropic resolution). Colored-in red and green areas reflect, respectively, changes in grey and white matter in the patients relative to scans from 201 control participants aged 40+ with no history of brain lesion. The changes were detected using voxel-based morphological analysis in SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/SPM5), and they are overlaid here on a standard multi-slice template in MRIcron. The images were first segmented into grey matter, white matter, and cerebro-spinal fluid (CSF), and the resulting tissue classes images were normalized without modulation (i.e., to compensate for the effect of spatial normalization). Images were smoothed with a Gaussian kernel. The analyses are based on sample t-tests with 3 covariates: healthy grey/white matter vs patient grey/white matter, age and gender. All areas are FWE corrected with p=0.05 and an extent threshold specifying that only significant blobs containing $\geq 100$ voxels be included in the lesion.

All patients had extinction, three patients additionally showed neglect of the contralesional hemi-field (MP, RH, RP). None of the patients had visual field losses. With the exception of MH, all patients had one or more strokes several years ago, which resulted in lateralized spatial attention deficits. MH’s lesions are a result of carbon-monoxide poisoning. A group of seven age-matched healthy volunteers did the same task as the patients. They were between 58 and 74 years old (Mean=65.4 years).

Neglect and extinction were measured using the Birmingham Cognitive Screen (www.bcos.bham.ac.uk). The patients showed lateralized deficits on the tests of extinction (impairment on bilateral versus unilateral finger movements) and neglect (cancellation task where the number of left to right side cancelled targets was assessed). A spatial deficit was defined as a spatial asymmetry in performance that was more than two standard deviations outside the levels generated by age matched control participants.

Apparatus

Stimuli were generated using a standard PC running e-Prime (version 1.2; Psychology Software Tools, Pittsburgh, PA) on a 19” color monitor. Viewing distance was about 80 cm. Eye movements were recorded with an Eyelink 1000
### Table 3.1: Patient details

<table>
<thead>
<tr>
<th>Lesion</th>
<th>Deficit</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>MH</td>
<td>right extinction around left intraparietal sulcus extending to the left occipito-parietal junction, right intraparietal, white matter lesion (left lentiform nucleus)</td>
<td>58</td>
</tr>
<tr>
<td>MP</td>
<td>left extinction, neglect right superior + middle temporal gyri, right superior and middle temporal poles, right precentral gyrus, right middle frontal gyrus: pars opercularis + orbitalis, rolandic operculum, right supramarginal gyrus, right angular gyrus, right insula + caudate</td>
<td>62</td>
</tr>
<tr>
<td>PF</td>
<td>left extinction bilateral superior + inferior parietal gyri, left angular gyrus, right postcentral gyrus, left putamen, right caudate, left thalamus</td>
<td>58</td>
</tr>
<tr>
<td>PM</td>
<td>left extinction right superior temporal gyrus, right angular + supramarginal gyrus, left angular + supramarginal gyrus, left postcentral gyrus (small), bilateral putamen + caudate</td>
<td>68</td>
</tr>
<tr>
<td>RH</td>
<td>right extinction, neglect left superior + middle temporal gyrus, left inferior frontal gyrus: pars opercularis, rolandic operculum, left supramarginal gyrus, left angular gyrus, left insula + caudate</td>
<td>76</td>
</tr>
<tr>
<td>RP</td>
<td>left extinction, neglect right mid-frontal, precentral, postcentral gyrus, right inferior parietal gyrus, right angular gyrus, right mid occipital lobe, right inferior frontal: pars opercularis, right mid temporal gyrus, right caudate, right putamen, right rolandic operculum, right insula, right parahippocampal gyrus</td>
<td>57</td>
</tr>
</tbody>
</table>
Figure 3.2: Lesion sites of the patients. Gray matter lesions are shown in dark gray, white matter lesions in light gray.
3 Feature-based selection in patients with spatial attention deficits

eyetracker (SR research) using the standard built-in saccade detection algorithm. Data were analyzed using Matlab (Mathworks, Natick, MA).

Stimuli, procedure and design

Two orientation singletons were presented in a homogenous field of oriented lines (24*16 elements). Each line was about 0.8 degrees long and 0.2 degrees wide. All lines were white, presented on a dark gray background. The orientation singletons were always horizontal and vertical. We varied their salience by changing the orientation of the background lines (+/- 55 degrees, +/-35 degrees and +/-45 degrees) relative to the vertical axis of the screen. Participants were instructed to make a direct saccade to only one of the orientation singletons (e.g., horizontal, the Target). There were three factors: 1) Hemi-field with the levels affected and unaffected1, 2) Target-Distractor configuration with the levels Target and Distractor in the same hemi-field and Target and Distractor in different hemi-fields; and 3) Target salience with the levels Target more salient than the distractor, Target less salient than the distractor and Target and Distractor equally salient. Figure 3.1 shows a schematic depiction of all three target salience levels with the distractor in the same hemi-field as the target. All conditions were randomly mixed within blocks.

Each trial started with the presentation of a fixation cross in the center of the screen (until stable fixation of at least 1 second), directly followed by the presentation of the search display (for 2 seconds). Drift correction was performed during the presentation of the fixation cross. The data were collected during four (control participants) or six (patients) appointments per participant. Each participant completed two blocks of 144 trials per appointment, with target orientation (horizontal or vertical) alternating between appointments. All seven control participants and five of the six patients completed 12 blocks of 144 trials each. Patient PM completed 8 blocks of 144 trials.

Data Processing

We analyzed the first saccade with a minimal latency of 80 ms and a maximal latency of 800 ms from search display onset and an endpoint of at least 2 degrees from fixation. Trials with eye blinks before the first saccade were excluded from the analysis. Since we were interested in the relative contributions of the salience of a singleton item and its behavioral relevance relative to the other singleton, we focused on trials in which the first saccade went into a quadrant containing an orientation singleton. We then sorted the remaining saccadic latencies that ended in the quadrant of either target or distractor in ascending order and binned them in five bins. Thus, the first bin contained the 20% fastest saccades to

1Note that we refer to affected and unaffected hemi-field on the basis of the results of the clinical tests. As neglect more often affects the left hemi-field, we compare the affected hemi-field of the patients to the left hemi-field of the controls and the unaffected hemi-field of the patients to the right hemi-field of the controls. We note that the controls tended to perform worse for targets in their left hemi-field, so treating this as the 'impaired' side provided a conservative analysis of the data.
either target or distractor; the last bin the 20% slowest saccades. We did this separately for each combination of hemi-field, target-distractor configuration and target salience, for each participant.

Model fitting

Based on a large number of previous findings (Jonides, 1981; Müller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987; van Zoest et al., 2004) we assume that selection is driven by two types of evidence available, both of which are illustrated in Figure 3.3:

1. Rapidly available, but slowly decaying salience information, thus transiently driving selection in an exogenous, bottom-up fashion (Dombrowe, Olivier, & Donk, 2010b; Donk & Soesman, 2010). Within the model, the probability that the system is biased towards the most salient element in the display on the basis of stimulus-driven processes, $S(t)$, is depicted in Figure 3.3 and is given by the function

$$S(t) = e^{-rate_S \times (t-time_{0S})}$$

with $rate_S$ reflecting the rate of decay (i.e. the slope) and $time_{0S}$ indicating the start of the function, in this case reflecting the moment in time at which the salience-driven bias is maximal.\(^2\) Note that the above-mentioned studies actually assume that it takes some time (between 100 and 200 ms) for bottom-up activation to reach this peak level. However, we decided not to model this rapidly rising first part of the function, as it would require an additional set of parameters none of which could be estimated, given that we had no datapoints in this range. The function ranges from 1 to 0, with 1 indicating that the probability that the system is biased towards the more salient element as maximal, and 0 indicating that this probability is minimal.

2. More slowly developing, but gradually increasing information on target identity, thus driving selection in a more sustained and endogenous, top-down fashion. Within the model, the probability that the system is biased towards the target on the basis of goal-driven processing as a function of time, $G(t)$, is given by the function

$$G(t) = 1 - e^{-rate_G \times (t-time_{0G})}$$

with $rate_G$ reflecting the rate at which the function builds up (i.e. the slope), and $time_{0G}$ indicating the onset of the function. Also this function ranges between 0 and 1.

At each point in time, overt visual orienting is assumed to be determined by a $S(t)$ and $G(t)$, both of which vary between 0 and 1. Even though it is impossible to directly observe the extent to which each of these biases contribute to

\(^2\)An exponential function was chosen for mathematical simplicity, and because neuronal activity can be approximated by a poisson process (Townsend & Ashby, 1983).
Figure 3.3: G(t) indicates the probability that the system is biased towards the target on the basis of goal-driven processes. S(t) indicates the probability that the system is biased towards the most salient singleton on the basis of stimulus-driven processes.

selection, it is possible to infer their relative contribution by fitting the observed proportions of correct target saccades in each condition to the multinomial tree model presented in Figure 3.4 (see Batchelder & Riefer, 1999).

In each tree, G(t) indicates the probability that the system is biased towards the target on the basis of goal-driven processes at time t, and S(t) indicates the probability that the system is biased towards the most salient element in the display on the basis of salience-driven processes at time t. 1-G(t) that the system is unbiased by goal-driven processes and 1-S(t) indicates that the system is unbiased by stimulus-driven processes. Black circles in Figure 3.4 indicate a correct outcome (i.e. when the target is selected).

The outcome on each trial (i.e. either a correct saccade to the target or an incorrect saccade to the distractor) is represented as one path from the central node at the left of each tree to the response category at the right of each tree (as indicated by the color of the rightmost node: filled = correct saccade to the target, empty = incorrect saccade to the distractor). The probability that the response of an observer follows a particular path on a certain trial is given by the product of the individual probabilities in this path. For instance, if the target is more salient than the distractor and observers are affected by both goal-driven bias and a stimulus-driven processes with a probability G(t) and S(t), respectively, they will
Figure 3.4: Binomial trees for the three target salience levels.
correctly saccade towards the target with a probability that equals $G(t) \ast S(t)$. The overall probability of a correct saccade in a specific condition can be determined by adding the probabilities of all branches leading to a correct saccade. Each of these branches represents one theoretically possible correct outcome. For example, when the target is more salient than the distractor, the probability of a correct saccade is given by $P(\text{correct saccade}) = (G_t \ast S_t) + ((1-G_t) \ast S_t) + ((1-G_t) \ast (1-S_t) \ast 0.5)$. In other words, whenever the target is more salient than the distractor, the correct response is given by the presence of a stimulus-driven bias ($S(t)$), a goal-driven bias ($G(t)$), or both. In addition, if observers are unaffected by biases, the model predicts the probability of a saccade to the target to be equal to that of a saccade towards the distractor, i.e., .5.

When the target is less salient than the distractor and observers are affected by both salience-driven and goal-driven biases, they are confronted with conflicting tendencies. That is, the salience-driven bias drives the system towards an incorrect saccade to the distractor, whereas the goal-driven bias actuates a correct saccade to the target. In such a case, the observer’s response might be based on either one or the other bias. Because it is impossible to determine a priori which one of the biases affects selection when there is a conflict, we introduced an additional model parameter $G_{bias}$ which indicates the probability that $G(t)$ prevails over $S(t)$. The $G_{bias}$ ranges from 0 ($S(t)$ prevails over $G(t)$ resulting in an incorrect saccade towards the more salient distractor) to 1 (when $G(t)$ prevails over $S(t)$ resulting in a correct saccade to the target).

In cases where the target and the distractor are equally salient, visual selection is entirely goal-driven. This means that whenever observers are biased on the basis of goal-driven processes, a saccade to the target will occur. When observers are not affected by goal-driven biases ($1 - G(t)$), the probability of a saccade to the target is .5.

The model was fit separately to the data of each participant. Each dataset consisted of 15 data points (average proportions correct), with 5 data points for each target salience level (i.e., a 5 (bins) * 3 (target salience) matrix).

We estimated the model parameters $rate_G$, $time_{0G}$, $rate_S$, $time_{0S}$ and $G_{bias}$ for each of the participants using Maximum Likelihood Estimation (MLE), with the following constraints: $0 \leq rate_G \leq 0.05, 0 \leq time_{0G} \leq 800, 0 \leq rate_S \leq 0.05, 0 \leq time_{0S} \leq 800$ and $0 \leq G_{bias} \leq 1$.

The maximum likelihood estimates are those parameter values that minimize $-\log(E)$ in which $E$ is given by

$$E = \prod_{i,j} \left( \frac{n_{i,j}}{c_{i,j}} \right) \ast p_{i,j}^{c_{i,j}} \ast (1 - p_{i,j})^{n_{i,j} - c_{i,j}}$$

with $n$ denoting the total number of eye movements per bin and $c$ the number of eye movements that went to the target for each target salience level $i$ and bin $j$. The parameter $p$ indicates the probability that an eye movement ends on the target given the model. $-\log(E)$ was minimized using the Matlab function fmincon. Starting values for the parameters covered the whole range of possible
parameter values (e.g. starting values for rate\(_G\) were chosen from 0 to 0.05 in steps of 0.01).
Finally, we computed the areas under the curves for G(t) and S(t), respectively in the interval from 0 ms to 800 ms in order to capture the total contribution of each process within this time interval. For S(t), the decaying function, this included the time up to time\(_0\).

Results and Discussion of Experiment 1

In the following section, we first present the results of the healthy control participants. We then compare the results of the patients to those of the control group. We further compare top-down and bottom-up processing in the affected hemi-field to processing in the unaffected hemi-field of the patients. Since we were interested in directly comparing the relative sparing of top-down and bottom-up processing in the affected hemi-field, we focussed on those trials in which both items (i.e. target and distractor) were present within one hemi-field. Trials in which target and distractor were presented in different hemi-fields were more difficult to analyze because of the overall spatial biases of some of the patients (see below). These trials will be briefly discussed at the end of the section.

Healthy control participants

Eye movement data

Of those trials in which target and distractor were in the same hemi-field, 96.7% of the first saccades ended up in this hemi-field, with the remaining 3.3% ending up in the other hemi-field.
Of these 96.7%, Figure 3.5 shows the proportion of first saccades correctly directed to the target for all trials in which the target and distractor were presented in the left hemi-field (upper panel of Figure 3.5) or in the right hemi-field (lower panel of Figure 3.5). An ANOVA with the factors hemi-field (left, right), target salience (target more salient, target less salient, target and distractor equally salient) and bin (1-5) revealed that overall performance was better when target and distractor were presented in the right hemi-field (Mean = 0.6500) than when they were presented in the left hemi-field (Mean = 0.6031, F(1, 6) = 11.590, \(p < 0.05\)). Performance improved with increasing saccadic latency (main effect of bin, F(4, 24) = 10.679, \(p < 0.01\)). Further, performance was best when the target was more salient than the distractor (Mean = 0.6031, F(2, 12) = 11.590, \(p < 0.01\)) and worst when the target was less salient than the distractor (Mean = 0.4446; main effect of target salience, F(2, 12) = 18.729, \(p < 0.01\)). These differences decreased with increasing saccadic latency, as confirmed by the interaction of target salience and bin (F(8, 48) = 14.991, \(p < 0.001\)). The remaining interactions were not significant.
An ANOVA on saccadic latencies with the factors hemi-field (left, right), target salience (target more salient, target less salient, target and distractor equally salient) did not reveal any significant effects. Thus, the healthy elderly participants showed a very similar time course of saccadic visual selection to healthy
Figure 3.5: Proportions of first saccades to the target as a function of saccadic latency. The upper panel depicts the first saccades into the left hemi-field, the lower panel the first saccades into the right hemi-field. Asterisks indicate a significant difference from chance level (.5) as determined by a two-tailed t-test; **$p < 0.01$, *$p < 0.05$.

Legend: —●— Target more salient than the distractor, —+— Target and distractor equally salient, —■— Target less salient than the distractor.
young university students, such that short-latency saccades were predominantly stimulus-driven and were more likely to end on the most salient element in the display, whereas saccades became more goal-driven with increasing saccadic latency (van Zoest et al., 2004; van Zoest & Donk, 2005, 2008).

### Fitting the model

To assess the relative contributions of the top-down and bottom-up processes to the individual performance of each control participant, we fitted the multinomial model described in the methods section. In addition to estimating the model parameters for each type of bias ($rate_G$, $time_{0G}$, $rate_S$, $time_{0S}$, $G_{bias}$), we computed the area under the top-down function ($area_{TD}$) as well as under the bottom-up function ($area_{BU}$). These areas provided us with simple measures that captured how much either of both biasing processes contributed to visual selection within the interval between 0 and 800 ms.

Figure 3.6 shows the model fits for the control participants. Table 3.2 lists the parameter values and areas under the curves for each participant. Paired, two-

<table>
<thead>
<tr>
<th>Left hemi-field</th>
<th>rate$_G$</th>
<th>time$_{0G}$</th>
<th>rate$_S$</th>
<th>time$_{0S}$</th>
<th>$G_{bias}$</th>
<th>area BU</th>
<th>area TD</th>
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<td>PB</td>
</tr>
<tr>
<td>PT</td>
</tr>
<tr>
<td>RW</td>
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</table>

Table 3.2: Model parameters and areas for the healthy, elderly control participants.

tailed t-tests on the model parameters and areas showed that the TD area for the left hemi-field was smaller than the TD area in the right hemi-field ($t(6) = 2.806$, $p < 0.05$). This effect was driven by two participants, GL and NM, who showed considerably less top-down processing of stimuli in the left hemi-field. All other t-tests failed to reach significance.

An analysis of the model fits suggested that the performance of control participants GL and NM with stimuli in the left hemi-field did not follow the pattern described by the model ($R^2$'s of 0.28 and 0.06, respectively). The remaining model fits were quite good with an average $R^2$ of 0.66 for performance with stimuli in the left hemi-field and an average of $R^2$ of 0.68 for performance with stimuli in the right hemi-field, in particular with respect to the fact that the model describes individual data patterns consisting of fifteen data points with
Figure 3.6: Model fits for the control participants. Left panels: Target and distractor in the left hemi-field, right panels: Target and distractor in the right hemi-field.

Legend: ○ Target more salient than the distractor, × Target and distractor equally salient, □ Target less salient than the distractor.
just five free parameters.

Patients

Selection of any item: Time dependent spatial biases

As for the control participants, we were interested in the relative contributions of bottom-up and top-down processes to saccadic selection. However, as expected, not all patients always correctly chose the hemi-field containing these items for the first saccade, but often made a saccade into the hemi-field that contained only background items instead. Therefore, we first determined the proportion of saccades that were correctly directed to the hemi-field that contained the target and the distractor. We then sorted the latencies of these saccades in ascending order and binned them in five bins. Figure 3.7 shows the proportion of saccades that ended in the hemi-field containing target and distractor for each bin of each patient. The left panel of Figure 3.7 depicts the data for trials when target and distractor were presented in the affected hemi-field, the right panel of Figure 3.7 the data of the trials when both items were presented in the unaffected hemi-field. An ANOVA with the factors hemi-field (affected, unaffected for patients; left, right for controls) and bin (1-5) as within-subjects factors and group (patients, controls) showed that the overall accuracy of the patients (Mean = 0.784) was lower than that of the controls (Mean = 0.967, main effect of group, F(1, 11) = 37.150, p < 0.001). Further, accuracy increased with increasing saccadic latency (main effect of bin, F(4, 44) = 19.008, p < 0.001). This effect was stronger for the patients than for the controls (interaction of group and bin, F(4, 44) = 7.675, p < 0.01).

As Figure 3.7 illustrates, two of the patients (MP and RH) showed a time-dependent bias away from their affected hemi-field (upper panel), the hemi-field in which they showed neglect in clinical tests. A large majority of the short latency saccades of these patients were directed away from the affected hemi-field when target and distractor were presented in the neglected hemi-field. This bias ameliorated over time, such that saccades with longer latencies were directed towards the affected hemi-field. Nevertheless, their overall accuracy remained lower than that of the other patients. We found a similar pattern for the unaffected hemi-field (lower panel of Figure 3.7). Here, two different patients (PM and MH) showed a time-dependent bias away from their unaffected hemi-field. This finding was surprising, since both target and distractor were presented in the hemi-field unaffected by extinction in clinical tests, and may therefore reflect a compensatory mechanism. An ANOVA on the saccadic latencies with the factors hemi-field (affected, unaffected for patients; left, right for controls) and group (patients, controls) did not reveal any significant effects.

Impaired top-down and bottom-up feature-selection in the affected hemi-field

Next, we analyzed those trials in which the participants made a saccade to one of the two singletons. Figure 3.8 depicts the proportion of correct saccades as
Figure 3.7: Proportion of first saccades directed to the correct hemi-field as a function of saccadic latency. Black lines indicate the data of the control participants, the data of the patients are depicted in gray. The upper panel shows the first saccades into the affected hemi-field, the lower panel shows the first saccades into the unaffected hemi-field.
a function of latency and hemi-field, provided that an eye movement had been made to either the target or the distractor. Thus, a proportion of .75 indicates that on 75% of those trials, the target was correctly selected (and on 100%-75% = 25% the distractor was selected). An ANOVA with the factors hemi-field (affected, unaffected), target salience (target more salient, target less salient, target and distractor equally salient) and bin (1-5) revealed that performance was best when the target was the most salient element in the display (Mean = 0.701), intermediate when target and distractor were equally salient (Mean = 0.516), and worst when the target was the least salient element in the display (Mean = 0.377; main effect of target salience, F(2, 10) = 54.708, p < 0.001). This effect was stronger in the unaffected hemi-field than in the affected hemi-field (interaction of hemi-field with target salience, F(2, 10) = 24.637, p < 0.01), although it was not completely absent in the latter (two-tailed t-test v. .5 at the first bin; target salient vs. .5: t(5)=2.766, p < 0.05, target less salient vs. .5: t(5)=4.5, p < 0.01). The difference between the salience levels decreased over time (interaction of target salience and bin, F(8, 40) = 6.250, p < 0.01). The remaining main effects and interactions were not significant.

An ANOVA on the saccadic latencies with the factors hemi-field (affected, unaffected) and target salience (target more salient, target less salient, target and distractor equally salient) did not reveal any significant effects.

To compare the patients to the controls, we performed an additional ANOVA with the same within-subjects factors as mentioned above and participant group (patients, controls) as a between-subjects factor. Since four out of six patients were (most) affected in their left hemi-field, we grouped the left hemi-field of the controls with the affected hemi-field of the patients. This showed that overall, performance increased with increasing saccadic latency (main effect of bin, F(4, 44) = 10.524, p < 0.01). Performance was worse in the affected hemi-field of the patients and in the left hemi-field of the controls than in the unaffected hemi-field of the patients and in the right hemi-field of the controls (main effect of hemi-field, F(1, 11) = 13.000, p < 0.01). Performance was best when the target was the most salient element, intermediate when target and distractor were equally salient, and worst when the target was the least salient element (main effect of target salience, F(2, 22) = 47.475, p < 0.001). The differences between the target salience levels decreased with increasing saccadic latencies (interaction of target salience with bin, F(8, 88) = 18.388, p < 0.001). The salience effect also varied across hemi-fields. The difference in target salience levels was more pronounced in the unaffected and right hemi-field than in the affected and left hemi-field (interaction of hemi-field with target salience, F(2, 22) = 19.456, p < 0.001) and was especially pronounced for the patients (three-way interaction of hemi-field and target salience with group, F(2, 22) = 10.647, p < 0.01). No other main effects or interactions were significant. We then fitted our model to the patient data. Individual fits are shown in Figure 3.9. Table 3.3 lists the model parameters together with the areas for each hemi-field of each patient, Figure 3.10 depicts the average areas for the controls, the average areas for the patients, as well as the areas for each patient individually. Two-tailed paired t-tests showed that bottom-up processing decreased faster when target and distractor
Figure 3.8: Performance of the patients as a function of saccadic latency. The upper panel shows the performance of the patients with both singletons in the affected hemi-field, the lower panel the performance of the patients with both singletons in the unaffected hemi-field. Asterisks indicate a significant difference from chance level (.5) as determined by a two-tailed t-test; ** \( p < 0.01 \), * \( p < 0.05 \). Legend: — Target more salient than the distractor, — Target and distractor equally salient, — Target less salient than the distractor.
were presented in the affected hemi-field than when they were presented in the unaffected hemi-field (rate\(_G\) affected hemi-field vs. rate\(_G\) unaffected hemi-field, t(5) = 2.848, p < 0.05). Overall, bottom-up processing contributed less to saccadic visual selection in the affected hemi-field than in the unaffected hemi-field (comparison of BU areas, t(5) = 7.258, p < 0.01). Further, five of our six patients showed a reduction in top-down processing of stimuli in the affected hemi-field relative to the unaffected hemi-field. For these patients top-down processing was slower in the affected hemi-field in comparison to the unaffected hemi-field (rate\(_G\) affected vs. rate\(_G\) unaffected hemi-field, t(4) = 3.264, p < 0.05). This was reflected in a smaller TD area for the affected hemi-field than for the unaffected hemi-field (t(4) = 3.023, p < 0.05). One patient (RH, see also Table 3.3) showed slower top-down processing for stimuli in the unaffected hemi-field than for stimuli in the affected hemi-field. As this patient was the only one with a unilateral left lesion, the reversal could be an indication of a hemispheric imbalance in directing goal-driven attention (see e.g. Mesulam, 1999).

A direct comparison to the control participants further confirmed these results. Both bottom-up and top-down processing were reduced when target and distractor were presented in the affected hemi-field of the patients (in comparison to the left hemi-field of controls, comparison area BU: t(11) = 2.886, p < 0.05, comparison area TD: t(11) = 2.663, p < 0.05). Specifically, their top-down processing tended to be delayed as indicated by a slower increase of G(t) and a later onset of this factor (comparison of rate\(_G\), t(7.358) = 2.243, p = 0.058, degrees of freedom corrected for unequal variances; comparison of time0\(_G\), t(4.887) = 2.340, p = 0.053, degrees of freedom corrected for unequal variances).

Further, top-down processing was also reduced in comparison to the control participants even when target and distractor were presented in the unaffected hemi-field (comparison area TD: t(11) = 2.327, p < 0.05). In particular, top-down processing tended to be slower than that of controls (comparison rate\(_G\), t(11) = 2.922, p < 0.05). Bottom-up processing of stimuli in the unaffected hemi-field (right hemi-field of the controls) was similar in patients and in controls (comparison area BU: t(11) = 0.561, p > 0.5).

Taken together, the results show that some relative salience information is available in the affected hemi-field, however less so than in the unaffected hemi-field. Furthermore, top-down guidance is more generally affected in that it develops only slowly in both hemi-fields of the patients, but is especially delayed in the affected hemi-field.

**Target and distractor in different hemi-fields**

Finally, we analyzed the trials on which target and distractor were presented in different hemi-fields. Note that these analyses are limited by overall spatial biases that the patients might have (as discussed above, see Figure 3.7). Three of six patients (MP, RH, MH) almost always made a saccade into the unaffected hemi-field, irrespective of where the target was presented. We fit our model to the data of the remaining three patients (RP, PF, PM) and computed the areas under G(t) and S(t). Table 3.4 lists the parameters together with the areas for these
Figure 3.9: Model fits for the patients.
Legend: ○ Target more salient than the distractor, × Target and distractor equally salient, □ Target less salient than the distractor.
### 3.2 Experiment 1

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<th>( \text{time}_S )</th>
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Table 3.3: Model parameters and areas under the curves for the patients.

Figure 3.10: Area BU and area TD for the control participants and the patients in the affected hemi-field are depicted on the left, areas for the unaffected hemi-field on the right. Data of control participants are shown in black with error bars. Average patient data are shown in dark gray with error bars. Error bars represent +/- one standard error of the mean. Labels refer to individual patients as listed in Table 1.
3 Feature-based selection in patients with spatial attention deficits

patients. All of these patients showed a faster decay of bottom-up processing

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<th>G_bias</th>
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<th>rate_S</th>
<th>time_0_S</th>
<th>G_bias</th>
<th>area BU</th>
<th>area TD</th>
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Table 3.4: Model parameters and areas for the patient group. Target and distractor were presented in different hemi-fields. Table headings refer to the hemi-field containing the target.

that started later in the affected hemi-field as compared to the unaffected hemi-field (compare the parameters rate_S and time_0_S for the different hemi-fields). In addition, RH, PF and PM showed a slower increase of top-down processing (parameter rate_G), two of them with a later onset (parameter time_0_G). Thus, again both top-down and bottom-up processing contributed less to the processing of stimuli in the affected hemi-field than in the unaffected hemi-field (as reflected in reduced area sizes for both area BU and area TD). This is consistent with the above findings, when target and distractor were presented both in the same hemi-field.

3.3 Experiment 2

Experiment 1 revealed deficits in both stimulus-driven and goal-driven selection of feature-defined objects in the affected hemi-field. That is, the patients were less able to exploit feature differences in choosing the target over the distractor than the controls. We assessed target selection on those trials on which observers had moved their eyes into the hemi-field containing the target and the distractor. However note that, compared to controls, the patients showed an overall bias away from their affected hemi-field (except PM and MH, who showed a compensatory bias towards their affected field). It is possible that the feature-based deficits measured in Experiment 1 depend on this spatial bias, in that the successful processing of bottom-up salience and top-down feature identity is contingent upon, or interacts with, spatial attention. Thus, we wanted to know if rectifying the spatial bias leads to any improvements regarding feature-based stimulus-driven or goal-driven processing.

In a second experiment, we therefore manipulated the overall spatial bias of the patients in three conditions. The Replication condition was designed to replicate the main condition of Experiment 1, in which the target and distractor were randomly presented together in either hemi-field. The patients were instructed to try to attend to both hemi-fields. In the Always-in-affected-field (background) condition, the target and the distractor were always presented in the affected hemi-field. Patients were informed about this and instructed to attend to this
hemi-field only. The unaffected hemi-field was filled with background items. The Always-in-affected-field (empty) condition was the same, but now the unaffected hemi-field was left completely empty. With these conditions, we wanted to maximally encourage the patients to attend more to the affected hemi-field, in order to see if this would improve bottom-up and top-down processing, or both.

**Methods**

All six patients of Experiment 1 also participated in Experiment 2. We used the same stimuli, procedure and design as in the previous experiment, with the following exceptions. In the Replication condition, the target and the distractor were either both presented in the affected hemi-field or both in the unaffected hemi-field. As in Experiment 1, hemi-field and target salience (target more salient, target less salient, target and distractor equally salient) were randomly mixed, now in blocks of 72 trials each. Prior to the block, patients received the instruction to try to attend to both sides. MH and PM explicitly received the instruction to try to attend also to their unaffected hemi-field (as they showed a bias away from this field in Experiment 1). Analyses showed that while PM indeed balanced his saccades more between hemi-fields, MH failed to do so and retained a strong bias towards the affected hemi-field. Since we were interested in the effects of a spatial bias away from the affected field, we had to exclude the data of this patient from further analysis. In the Always-in-affected-field (background) condition, the target and distractor were always presented in the affected hemi-field, and patients were instructed to only attend to this field. The unaffected hemi-field was filled with background items. The Always-in-affected-field (empty) condition was the same, but now the unaffected hemi-field was left completely empty. The latter two conditions were mixed in blocks of 72 trials each. In all, 24 blocks were run per patient.

**Results and Discussion**

We analyzed the data and fitted the model as for the previous experiment.

**Replication condition**

In the Replication condition, the pair of items (target and distractor) could appear in either hemi-field. As in the previous experiment, we first determined any spatial biases by looking at the proportion of saccades that were correctly directed to the hemi-field that contained the items, as a function of latency (bin). Figure 3.11 shows the proportion of saccades that ended in the hemi-field containing target and distractor for each bin of each patient. Four of the five patients made fewer saccades into their affected hemi-field. Statistically, this was expressed as a trend of hemi-field in an ANOVA with the factors hemi-field and bin ($F(1, 4) = 4.210, p = 0.109$). There was also a main effect of bin, as performance improved with time ($F(4, 16) = 3.671, p < 0.05$). To assess feature-based
Figure 3.11: Proportion of first saccades directed to the correct hemi-field as a function of saccadic latency in the *Replication* condition. The upper panel shows the first saccades into the affected hemi-field, the lower panel shows the first saccades into the unaffected hemi-field.
selection, we then analyzed those trials in which the participants made a saccade to either the target or the distractor. Figure 3.12 depicts the proportion of first saccades that were correctly directed to the target for those trials in which an eye movement was made to either the target and distractor, which were presented in the affected hemi-field (upper panel of Figure 3.12) or in the unaffected hemi-field (lower panel of Figure 3.12). An ANOVA with the factors hemi-field (affected, unaffected), target salience (target more salient, target less salient, target and distractor equally salient) and bin (1-5) revealed that performance was best when the target was the most salient element in the display (Mean = 0.662), intermediate when target and distractor were equally salient (Mean = 0.544), and worst when the target was the least salient element in the display (Mean = 0.392; main effect of target salience, F(2, 8) = 26.074, p < 0.01). Importantly, this difference was again more pronounced in the unaffected hemi-field (interaction of target salience with hemi-field, F(2, 8) = 8.733, p < 0.05) and decreased over time (interaction of target salience and bin, F(8, 32) = 3.206, p < 0.05). The remaining main effects and interactions were not significant.

An ANOVA on saccadic latencies with the factors hemi-field (left, right) and target salience (target more salient, target less salient, target and distractor equally salient) did not reveal any significant effects. Thus, the eye movement data replicated those of Experiment 1. An additional comparison with the same conditions of Experiment 1 did not reveal any significant interactions with Experiment (as a within subjects factor). Table 3.5 lists the model parameters together with the areas for each hemi-field of each patient. Paired t-tests on the areas showed that the TD area for the affected hemi-field was smaller than the TD area in the unaffected hemi-field (t(4) = 2.926, p < 0.05). Thus, top-down processing again contributed less to saccadic visual selection in the affected hemi-field than in the unaffected hemi-field. The same goes for bottom-up processing, which was reduced when target and distractor were presented in the affected hemi-field as compared to when they were presented in the unaffected hemi-field (BU area affected hemi-field vs. BU area unaffected hemi-field, t(4) = 2.131, p = 0.05; rate, affected vs. unaffected hemi-field, t(4) = 2.304, p < 0.05). We thus replicated our findings of Experiment 1.

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<th>rateS</th>
<th>timeS</th>
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Table 3.5: Model parameters and areas for the patients in the Replication condition of Experiment 2.
3 Feature-based selection in patients with spatial attention deficits

Figure 3.12: Proportion of first saccades directed to the correct hemi-field as a function of saccadic latency in the *Replication* condition. The upper panel shows the performance of the patients when both singletons were presented in the affected hemi-field, the lower panel shows the performance of the patients when both singletons were presented in the unaffected hemi-field. Asterisks indicate a significant difference from chance level (.5) as determined by a two-tailed t-test; \( **p < 0.01 \), \( *p < 0.05 \).

Legend: —●— Target more salient than the distractor, —★★— Target and distractor equally salient, —■— Target less salient than the distractor.
3.3 Experiment 2

Knowledge regarding target location improves spatial, but not feature-based selection

Of crucial interest in the present experiment were the conditions in which the items were always presented in the affected hemi-field, while the unaffected hemi-field was either empty (Always-in-affected-field [empty] condition) or contained only background items (Always-in-affected-field [background] condition). We found that all patients successfully used the top-down knowledge regarding the location of the target and directed almost all saccades into the affected hemi-field. In both conditions, the patients showed a significant improvement as compared to the Replication condition ([background]: F(1, 4) = 11.078, p < 0.05; [empty]: F(1, 4) = 11.116, p < 0.05).

As we did for the Replication condition, we then analyzed those trials in which the participants made their first saccade into the affected hemi-field. Figure 3.13 depicts the proportion of first saccades that were correctly directed to the target for all trials in which the target and distractor were presented in the affected hemi-field with background lines in the unaffected hemi-field (upper panel of Figure 3.13) or without background lines in the unaffected hemi-field (lower panel of Figure 3.13). The graphs suggest no change in performance when patients know the hemi-field containing the target, despite directing their first saccade into that field. Indeed, directly comparing the Always-in-affected-field conditions to the affected hemi-field of the Replication condition revealed no significant main effects or interactions. At the same time, a direct comparison to the unaffected hemi-field of the Replication condition again revealed significant reductions in the use of feature information in the affected hemi-field, as expressed by hemi-field × target salience interactions (unaffected hemi-field filled with background elements: F(2, 8) = 7.597, p < 0.05; unaffected hemi-field empty: F(2, 8) = 13.211, p < 0.05). Table 3.6 shows the model parameters together with the areas under the bottom-up and top-down functions for these conditions. Thus, top-down knowledge regarding the locations of the singletons did

<table>
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<th>rateS</th>
<th>timeS</th>
<th>Gbias</th>
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Table 3.6: Model parameters and areas for the patients in Experiment 2. Target and distractor were always presented in the affected hemi-field, while the unaffected hemi-field was either filled with background elements (with background) or was empty (without background).
Figure 3.13: Performance of the patients when both target and distractor were presented in the affected hemi-field. Asterisks indicate a significant difference from chance level (.5) as determined by a two-tailed t-test; *$p < 0.05$.

Legend: —●— Target more salient than the distractor, —+— Target and distractor equally salient, —■— Target less salient than the distractor.
not improve feature-based saccadic visual selection in our patients. Although information regarding the location of the items improved overall spatial orienting, it did not improve the use of stimulus salience or identity-based information within this hemi-field. We conclude that the reduced availability of bottom-up and top-down feature processing is not caused by a spatial bias away from the affected field. One may argue that the reverse is more likely: There is a bias away from the affected hemi-field because of damaged salience and identity processing.

3.4 General Discussion

The present study assessed the contribution of stimulus-driven and goal-driven processes to feature-based selection in patients with lateralized attention deficits, while taking the dynamics of these processes into account. Previous experiments with healthy participants have repeatedly shown that selection varies as a function of time, such that short-latency saccades are predominantly stimulus-driven whereas saccades with longer latencies are mainly goal-driven (van Zoest et al., 2004; van Zoest & Donk, 2005, 2006, 2008, 2010; Donk & van Zoest, 2008). This was again replicated here in an elderly control group. Together with other findings, these results suggest that visual selection is driven by two independent processes; a fast rising and slowly decaying stimulus-driven function and a gradually increasing goal-driven process (see e.g. Jonides, 1981; Müller & Findlay, 1988; Nakayama & Mackeben, 1989; Weichselgartner & Sperling, 1987).

Using this dissociation between stimulus-driven, and goal-driven processes as a basis for a formal multinomial model, we estimated the relative contribution of these processes to feature-based saccadic selection. This revealed a number of important findings:

1. The patients showed a reduced influence of stimulus-based processing in their affected hemi-field, relative to their unaffected hemi-field and to healthy controls. This was indicated by a reduced sensitivity to the relative salience difference between the target and distractor in this hemi-field. Stimulus-driven processing appeared largely intact in the unaffected hemi-field.

2. Although reduced, salience-based information was not completely eradicated. That is, relative salience did affect saccadic selection shortly after display onset, but then rapidly decayed. The finding that some information is available very early in time but not later is counterintuitive, and once more serves to demonstrate that stimulus-driven and goal-driven processes can be dissociated in time.

3. This rapid reduction in salience-based processing was not because it was overridden by stronger goal-based selection. In addition to impaired bottom-up processing goal-directed selection was also weaker than normal, and this was the case for targets falling in both hemi-fields. This suggests that
whereas salience is presented more retinotopically, goal-driven influences may operate more bilaterally, in line with a general attentional template.

4. None of these effects were modulated by the overall spatial bias towards or away from the affected hemifield, suggesting that feature selection does not depend on the spatial distribution of attention.

**Stimulus-driven selection**

Reduced effects of stimulus-driven processing of stimuli in the affected hemifield relative to the unaffected hemi-field have been observed before in spatial cueing tasks as well as in visual search (e.g. Posner et al., 1982, 1984; D’Erme et al., 1992; Lädavas et al., 1994; Smania et al., 1998; Natale, Posteraro, Prior, & Marzi, 2005; Bays et al., 2010). Our results fully match with these previous findings, as we found a reduced influence of stimulus-driven processes on visual selection for all patients. By fitting our model to the eye movement data, we were able to show that there was an initial transient stimulus-driven bias but this lost impact very soon after stimulus onset. This is important to note, because many tests of detection of stimuli in the contralesional hemi-field fail to take time into account, and may therefore lead to the incorrect conclusion that there is no bottom-up information available at all. Furthermore, whereas previous studies looked at the detection of single stimuli at various locations, our work shows that the reduction in salience processing also holds in a multiple object display when relative salience has to be computed between two items that stand out against a background.

Our results fit with the idea that neglect and extinction are associated with an uneven representation of salience across the visual field (Pouget & Driver, 2000; Driver & Vuilleumier, 2001). This theory receives further support from the results of several studies indicating that the representation of stimulus salience takes the form of a gradient that decreases from the periphery of the unaffected hemi-field to the periphery of the affected hemi-field (Cate & Behrmann, 2002; Behrmann, Watt, Black, & Barton, 1997). Attempts to counteract the gradient by increasing the overall stimulus salience in the affected hemi-field or decreasing the salience of the stimulus in the unaffected hemi-field have been quite successful (e.g. Di Pellegrino, Basso, & Frassinetti, 1997; Geeraerts, Michiels, Lafosse, Vandenbussche, & Verfaillie, 2005; Bays, Singh-Curry, Gorgoraptis, Driver, & Husain, 2010). For instance, Geeraerts et al. (2005) could eliminate extinction by strongly increasing the luminance of a stimulus in the affected hemi-field or decreasing stimulus luminance in the unaffected hemi-field. Di Pellegrino et al. (1997) achieved the same by using different stimulus-onset-asynchronies between two stimuli in different hemi-fields. Whenever the stimulus in the affected hemi-field led by about 200 ms, both stimuli were perceived as occurring simultaneously by a patient with extinction.

Some authors have argued that the salience representation of stimuli in the unaffected hemi-field is enhanced in comparison to the representation of stimulus salience in the healthy brain (e.g. Lädavas, Petronio, & Umiltà, 1990). The results of the present study suggest that this may need to be qualified. Although
our study is inconclusive as to whether sensory representations are overall enhanced in the unaffected hemi-field, or reduced in the affected hemi-field (an overall bias could simply reflect both), there was no sign that the relative salience between two items (target and distractor) was enhanced within the unaffected hemi-field in comparison the representation of the relative salience between two items in the healthy brain.

**Goal-driven selection**

In contrast to stimulus-driven selection, previous studies have often found goal-driven selection of stimuli in the affected hemi-field to be relatively intact (e.g. Lâdavas et al., 1994; Smania et al., 1998; Natale et al., 2005). Cueing studies, for example, have reported an improvement in performance for stimuli presented in the affected hemi-field when some implicit or explicit top-down information about target location (e.g. by cueing or blocked target presentation) is given, suggesting that some compensation for the reduced salience representation of stimuli presented in the affected hemi-field is possible whenever attention has to be directed in space (Posner et al., 1984; Riddoch, 1983). Experiment 2 supports this conclusion. When we told our patients that the target could always be found in their affected hemi-field, their bias towards the unaffected hemi-field disappeared. However, feature based selection of stimuli within the affected hemi-field was not improved by this manipulation. Although our patients now made more saccades into the affected hemi-field, they were not more successful in choosing the target over the distractor on the basis of orientation information, nor were they aided more if the target was more salient. This indicates that top-down information regarding the location of the target only improves spatial orienting, but not feature based-selection, suggesting a dissociation between the two types of selection.

We found reduced effects of goal-driven processing of stimuli in the affected hemi-field relative to the unaffected hemi-field for all but one of the patients. This patient (RH) was the only one with a pure unilateral left lesion. The remaining five suffered either from right or bilateral lesions. Two of the patients with right hemisphere lesions showed a contralesional reduction of top-down processing, and for three patients top-down processing of stimuli in the affected hemi-field was even completely absent. An analysis of top-down processing is often complicated by the fact that goal-driven processing can already vary considerably in the healthy control group (let alone between patients). Duncan, Bundesen, Olson, Humphreys, Chavda, & Shibuya (1999), for example, analyzed the performance of neglect and extinction patients in a partial report task in terms of the Theory of Visual Attention (TVA Bundesen, 1990), a task that requires feature-based selection. In their Experiment 2, participants were asked to report as many targets of a specified color as possible, while ignoring distractors of another color. As expected, their patients showed a bias towards the unaffected hemi-field when reporting the target items. They also differed from controls on a number of other TVA parameters, such as sensory effectiveness (C) and visual short-term memory (K, see Experiment 1 of Duncan et al.,
To their surprise, the parameter reflecting top-down feature-based selection weights ($\alpha$) did not differ between patients and the control group. As pointed out by Hung, Driver, & Walsh (2005), this could have been due to the large variability regarding this parameter in the control group. The fact that our patient RH differed from the other patients with regard to top-down processing might be due to a similar variability, or to the fact that he is the only patient with a unilateral left lesion.

Overall, our results indicate that goal-driven processing is impaired in neglect and extinction, although this may only be the case for right hemisphere lesions. Compared to the left hemisphere, the right hemisphere appears more involved in representing the general target template, from which selection is then biased across the visual field (i.e. both left and right).

Limitations

Our interpretation of the model fits is based on the assumption that the bottom-up and the top-down biases are independent from each other. This implies that the probability that the system is biased towards the target on the basis of goal-driven processes is assumed to be independent from the probability that the system is biased towards the most salient element on the basis of salience-driven processes. We cannot be sure that this assumption holds. However, the results of various studies suggest that bottom-up and top-down control might originate in different brain areas (e.g. Corbetta & Shulman, 2002; Posner & Petersen, 1990; Buschman & Miller, 2007). Further, a number of studies that have teased apart the unique influence of bottom-up and top-down factors in visual selection have found that these processes have distinct time courses (e.g. Fecteau, Bell, & Munoz, 2004; van Zoest et al., 2004). Our present data again provide evidence for this dissociation across time, because in the affected hemifield very early bottom-up selection was combined with very late goal-driven selection. Taken together, it seems reasonable to assume that both types of control are independent. We point out however, that even though bottom-up and top-down biases may reflect independent processes, in the end they both operate on the same incoming information and both will map onto the same response, here an eye movement. Trivial though this may be, it does mean that their effects on behavior will correlate: without a stimulus, or without some sensory representation to begin with, neither process will lead to selection.

The neuroanatomy of top-down and bottom-up attention

It is commonly assumed that the interplay of top-down and bottom-up attention is controlled by a network of brain areas in the parietal and frontal lobes (Posner & Petersen, 1990; Mesulam, 1999; Corbetta & Shulman, 2002; Corbetta et al., 2008; Bressler & Menon, 2010). A classic proposal of how this could be implemented in the brain was suggested by Posner and Petersen (1990). According to their account, goal-driven and stimulus-driven processing are carried out by distinct, anatomically separate sub-networks; an anterior and a posterior attention system. In particular, they identified the anterior cingulate gyrus with top-
down or goal-driven processing and the posterior parietal lobe with bottom-up or stimulus-driven processing. None of our patients is known to have damage to the anterior cingulate, and only three patients have some frontal lesions at all, making the anterior / posterior distinction an inconsistent explanation for our data.

Another possible subdivision of the frontoparietal attention network is between the dorsal and the ventral frontoparietal attention system (Corbetta & Shulman, 2002; He, Snyder, Vincent, Epstein, Shulman, & Corbetta, 2007; Corbetta et al., 2008). The dorsal system consists of the dorsal part of the parietal lobe and the dorsal frontal cortex. It is thought to be specialized in selecting and responding to visual stimuli. The ventral system involves the more inferior parts of the parietal lobe, including the TPJ and the ventral frontal cortex. This subsystem is assumed to act as an interrupt mechanism, which tells the posterior system that there is an object of interest to select or respond to. If this also includes information on the location of this object, the area around TPJ could indeed function as a priority map. The important question is then, whether this priority map would represent bottom-up information, top-down information (i.e. the target template), or an integration of both. Arguments have been made for all three possibilities (Corbetta & Shulman, 2002; Corbetta et al., 2008; Mavritsaki et al., 2010). For example, Mavritsaki et al. (2010) found evidence for a priority map in the area around TPJ that integrates top-down and bottom-up information. This map is supposed to receive top-down input from the more dorsal parietal regions. Given that the area around TPJ is the area of damage that almost all of our patients have in common, and given that they suffered from both top-down and bottom-up selection problems, our results also point to an integration function of the TPJ. The only exception would be MH, who had more superior lesions. However, since the inferior parietal areas are thought to communicate with the TPJ region, this is not inconsistent with our findings.

**Conclusion**

We conclude that feature-based selection, whether stimulus-driven or goal-driven, is substantially impaired in patients with lateralized spatial attention deficits. Whereas salience representations are initially available and affect fast saccades in both healthy controls and the patients, this type of selection is much weaker in the patients. The same goes for goal-driven selection, which is overall reduced in the patient group, except for the patient with the unilateral left lesion. Our results are in line with the view of the inferior parietal areas surrounding TPJ as integrating bottom-up and top-down feature information, thus providing the signal for where to look next.
The time course of working memory effects on visual attention.

Previous work has generated inconsistent results with regard to what extent working memory (WM) content guides visual attention. Some studies found effects of easy to verbalize stimuli whereas others only found an influence of visual memory content. To resolve this, we compared the time courses of memory-based attentional guidance for different memory types. Participants first memorized a color, which was either easy or difficult to verbalize. They then looked for an unrelated target in a visual search display and finally completed a memory test. One of the distractors in the search display could have the memorized color. We varied the time between the to-be-remembered color and the search display, as well as the ease with which the colors could be verbalized. We found that the influence of easy to verbalize WM content on visual search decreased with increasing time, whereas the influence of visual WM content was sustained. However, visual working memory effects on attention also decreased when the duration of visual encoding was limited by an additional task or when the memory item was presented only briefly. We propose that for working memory effects on visual attention to be sustained, a sufficiently strong visual representation is necessary.

4 The time course of working memory effects on visual attention

4.1 Introduction

Working memory and attention are closely related concepts: Working memory stores relevant information for later use, attention selects potentially relevant information. Within the visual domain, they share common neural resources (Mayer, Bittner, Nikolic, Bledowski, Goebel, & Linden, 2007; Awh, Vogel, & Oh, 2006; Chelazzi, Duncan, Miller, & Desimone, 1998), appear to have the same capacity limitation of about four objects (Cowan, 2001; Luck & Vogel, 1997), and interact with each other on several levels (see Olivers, 2008; Chun & Turkbrowne, 2007; Awh, Vogel, & Oh, 2006, for reviews). This study is concerned with how information about object features stored in working memory affects the allocation of visual attention.

The visual search task, in which observers are asked to find a target object among several distractor objects, has provided a popular tool for exploring the interactions between working memory and attention (see e.g. de Fockert, Rees, Frith, & Lavie, 2004; Downing & Dodds, 2004; Woodman & Luck, 2004). It is assumed that visual search is impaired when working memory interferes with visual attention, leading for example to slowed reaction times to the target. Since finding a target among distractors requires a representation of the search goal, many theories of visual search assume the existence of a target template in working memory (e.g. Desimone & Duncan, 1995; Bundesen, 1990; Duncan & Humphreys, 1989). The template biases the allocation of attention, such that objects in the visual field that share features with the target template are prioritized. Although this mechanism facilitates target selection, it also causes attention to be involuntarily attracted by features that match the current attentional set (i.e. target template), but do not belong to the search target (Folk, Remington, & Johnston, 1992). Thus, a distractor that shares features with the search target can involuntarily capture attention. However, it is still controversial if working memory content that is irrelevant for the search task can likewise cause the capture of attention in an involuntary manner. The presence or absence of unrelated memory effects on attention provides a stronger test of the relationship between the two constructs. Can a working memory item automatically guide attention when it is irrelevant for the search task and top-down guidance would be detrimental to search performance? Or can observers ignore working memory content when it interferes with the task at hand?

Many previous experiments addressing this question have shared a very similar design consisting of a visual search task interwoven with a memory task (e.g. Downing & Dodds, 2004; Olivers, Meijer, & Theeuwes, 2006; Houtkamp & Roelfsema, 2006; Soto & Humphreys, 2007, 2008; Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Rotshtein, 2007; Woodman & Luck, 2007). Participants typically first memorized a simple color, shape, or both, and then looked for an unrelated target in a visual search display. Finally, they completed a memory test. All studies compared (among other things) a condition where the memory item reappeared as an irrelevant distractor in the search task to a condition where all distractors of the search display were unrelated to the memorized item. The idea is that a distractor matching the content of memory may
interfere more than an unrelated distractor, as evidenced by increasing search RTs. This would be evidence for working memory automatically guiding attention.

However, results have been inconsistent. One important discrepancy concerns the assumed nature of the memory representation which interferes with attention. As working memory has been traditionally said to comprise separate sub-systems for verbal and visual information that selectively interfere with verbal and visual tasks, respectively (see e.g. Jonides, Lewis, Nee, Lustig, Berman, & Moore, 2008; Repovs & Baddeley, 2006; Baddeley, 2003, 1996; Logie, 1990), it would be reasonable to assume that only visual working memory interferes with visual attention. Consistent with this, Olivers et al. (2006) found that a distractor matching the remembered color only interfered with search when the color was very difficult to categorize semantically or verbally (because it had to be distinguished from only subtly different colors within the same category, e.g. different shades of red). Olivers et al. assumed that the difficult categorization would force observers to adopt a more visual memory representation. Indeed, a memory-matching distractor did not interfere when categorization was easy (because the color had to be distinguished from other canonical colors, e.g. green and blue). Olivers et al. assumed that under easy categorization conditions, it would suffice to convert the initial visual representation into a verbal code, that would then not interfere with the visual attention task. In support of such verbal re-labeling, Olivers (2009) found that even easy to categorize colors caused interference when verbal coding was prevented by an articulatory suppression task.

In contrast, Soto and colleagues (Soto et al., 2005; Soto & Humphreys, 2007) found interference of memory-matching distractors despite the fact that the memory content was easy to categorize, or was even presented verbally and without articulatory suppression tasks. In their task observers were presented with simple shapes (e.g. square, triangle) in canonical colors (e.g. red, green or blue) or verbal descriptions thereof. These colors could return in the search display presented shortly after. The memory test consisted of a single object which could be identical or different from the object, or differ in either shape or color category. Nevertheless, a memory match affected visual search.

The crucial factor here might be timing. In the original studies of Soto and colleagues the time between the onset of the to-be-memorized item and the search display (SOA) was relatively short, in the order of 300 ms. On the other hand, Olivers et al. (2006) typically used SOAs in the order of three seconds. More time between the memory item and the search display could have several effects depending on whether or not the item is easy or difficult to verbalize. For example, more time may allow for the transition of an initially visual representation of the to-be-memorized item to a more verbal representation, when such items are easily verbalizable. As a consequence, the memory effects on the visual search task may decrease with time. At first sight, this may appear at odds with Soto and Humphreys’ (2007) finding that even a completely verbally presented item can affect visual attention. However, it has been suggested that a word can induce a visual representation (e.g. Richter & Zwaan, 2009). Alternatively, with
completely verbal stimuli, a match may occur at a conceptual level. Such effects have been shown to be transient in nature (Huettig & Altmann, 2005). In contrast, when memory items are difficult to categorize or articulatory suppression is used, a stronger visual memory needs to be created, and memory effects may be more sustained. We explored this in Experiments 1 and 2. To foreshadow the results, easy to verbalize working memory content affected visual attention only at the shorter SOAs, whereas visual working memory content had a sustained effect on attention. We confirmed this finding in Experiment 3, in which we used articulatory suppression to prevent participants from verbalizing the working memory content.

An increased duration between the memory item and the search display may also allow for better encoding of the memory item, especially if the presentation duration is also extended. This would result in more sustained effects. We tested this directly in Experiment 4 by preventing subjects from further encoding the to-be-remembered color. We did this by presenting an additional rapid serial visual presentation task on the memory cue. Experiment 5 tested the prediction that shortening the presentation duration should lead to similar decrements. The results suggest that for sustained memory effects to occur, the memory item needs to be perceptually available for several hundreds of milliseconds.

By varying the timing we could also investigate another discrepancy in the literature on memory-based attention effects. Whereas Olivers et al. (2006) and Soto et al. (2005) found evidence for interference caused by distractors matching the content of memory, Woodman and Luck (2007) found no sign of interference. If anything, they found a facilitation of memory-matching distractors in search. Woodman and Luck argued that observers have control over their memory content and can use it to guide attention away from irrelevant items in visual search. Among other things, their experimental procedure differed in terms of timing from those of Soto et al. (2005) and Olivers et al. (2006). We therefore also included the timing parameters of Woodman and Luck (2007) to see if these could explain their findings.

4.2 Experiment 1: The time course of more verbal working memory effects on attention

Participants performed a visual search task bracketed by a memory task. Figure 4.1 depicts the procedure of one trial. They first memorized the color of a disk, then looked for a diamond among several colored disks and finally completed a memory test for the memorized color. In the memory test, the to-be-remembered color had to be distinguished from different color categories (e.g. red among blue and green). This made it in principle sufficient for the participant to just remember the color name, without having to remember a specific shade. Hence, from here on, we will refer to this condition as the “more verbal” memory condition. The memorized color randomly reappeared as a distractor in the search display on 50% of the trials. We varied the SOA between the to-be-remembered color and the search display in three step sizes (short, medium and long), such that they approximately matched the SOAs of the previous studies by Soto et al.
4.2 Experiment 1: The time course of more verbal working memory effects on attention

(2005), Woodman and Luck (2007), and Olivers et al. (2006). Following these studies, the presentation durations of the memory items varied accordingly. On the basis of the previous results of Soto et al. (2005) and Olivers et al. (2006), we expected interference to be reduced with increasing SOA.

Methods

Participants

Ten university students aged 18 to 44 years (Mean= 22) participated for course credit or money. They all reported having normal or corrected to normal acuity and color vision. The data of two participants were excluded from the analysis, because they made more than 43% and 28% errors in the search task.

Apparatus

An HP Compaq d530 CMT Pentium IV computer running E-Prime (Psychology Software tools, 2003) generated the stimuli on an Iiyama Vision Master Pro 454 SVGA 120-Hz screen and acquired the necessary response data through the standard keyboard. The experiment was run in a dimly lit room at a viewing distance of about 80 cm. All stimuli were presented on a black background (0 cd/m²).

Stimuli, procedure and design

Each trial started with the presentation of a fixation cross. After 500ms a colored disk (radius 1.5°) appeared in the center of the screen for either 150ms, 500ms or 1000ms (cue duration). This disk could be red, green, blue, yellow or purple. To match conditions in Experiment 2, the specific hue and chroma of each color could vary randomly between nine different combinations chosen on the basis of (though not exactly matching) the Munsell (1929) color system. The luminance of each color was kept constant at around 13 cd/m², except for yellow, which was brighter (42 cd/m²) in order to make it appear less brown. Participants were instructed to remember the color of the disk until the end of the trial.

After a variable stimulus-onset-asynchrony (SOA), a search display consisting of seven colored disks (radius 1.2°) and one diamond (diagonal 3.0°) appeared on the screen. They were placed on the outline of an imaginary circle (radius 5.3°, centered on fixation). We used three different SOAs: short (300ms with 150ms cue duration / 150ms ISI), medium (1000ms with 500ms cue duration / 500ms ISI) and long (3500ms with 1000ms cue duration / 2500ms ISI), approximately following the parameters of Soto et al. (2005); Woodman & Luck (2007); Olivers et al. (2006), respectively.

There were two different distractor type conditions. In the identical condition, one of the disks in the search display had the same color as the previously presented disk. All other items in the search display were randomly colored with each color appearing maximally twice. Gray was used as an additional color for the distractor disks and the diamond, but never for the critical distractor. In the
unrelated condition, one of the disks in the search display had a random color (except gray) that was different from the color of the previously presented disk. Each of the other eight items had one of the remaining four colors. In total, there were nine possible colors for the seven remaining elements in the display. Participants were instructed to search for the diamond and report whether there was an N or M inside by pressing the respective key. Each distractor contained an hourglass symbol ($|X|$) matching the line segments of the letters N and M. The search display remained on the screen until the participant made a response. Then, 500ms after the participant’s response a centrally presented row of three disks appeared on the screen. One of the disks matched the color of the first disk. The colors of the other disks were randomly chosen from the remaining color categories. Below the disks were the numbers 1, 2 and 3. Participants were instructed to indicate the number of the remembered color by pressing the respective key on the keyboard. An incorrect response was followed by a 250-ms feedback message saying “wrong”. Each trial ended with a blank screen of 1500ms. Figure 4.1 depicts one trial of Experiment 1. Participants first

Figure 4.1: Schematic representation of a trial of Experiment 1.

completed three practice blocks of 20 trials, with decreasing SOAs. Only in these practice blocks, the fixation cross was replaced by the instruction remember, and the instruction search was inserted between the memory item and the search display. The main experiment consisted of nine randomized blocks, three for each SOA. Each block consisted of 20 trials, with 10 trials for each of the two
4.3 Experiment 2: The time course of more visual working memory effects on attention

distractor type conditions. Thus, the experiment consisted of 180 trials in total.

Results and Discussion

<table>
<thead>
<tr>
<th>SOA (ms)</th>
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<th>1000</th>
<th>3500</th>
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<td>3.8%</td>
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<tr>
<td>unrelated</td>
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<td>1.7%</td>
<td>3.8%</td>
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<td>memory test</td>
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<tr>
<td>identical</td>
<td>5.0%</td>
<td>2.9%</td>
<td>1.3%</td>
</tr>
<tr>
<td>unrelated</td>
<td>2.1%</td>
<td>1.3%</td>
<td>2.1%</td>
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</table>

Table 4.1: Error percentages for the search and memory tasks in Experiment 1 as a function of SOA and similarity of the visual distractor to the memory item.

Participants made few errors on the search task (M=3.1%) and the memory test (M=2.9%). Table 4.1 shows the error percentages for each condition and SOA. An ANOVA with distractor type (identical, unrelated) and SOA (short, medium, long) as factors did not reveal any effects of either factor or the interaction in the search task or the memory test.

We iteratively trimmed RT data using the method of van Selst and Jolicoeur (1994). This resulted in the loss of 3% of all trials. We analyzed RTs for the remaining trials on which both responses were correct by performing an ANOVA with distractor type (identical, unrelated) and SOA (short, medium, long) as factors. Figure 4.2 shows the mean RTs for each of the distractor types as a function of SOA. Overall, participants were slower when the memorized color reappeared in the search task (identical: M=938ms) than when it did not (unrelated: M=889ms) [F(1,7)=44.186, p < 0.0001]. This effect was largest for the short SOA (89ms) and decreased with increasing SOAs (medium: 54ms, long: 3ms) [distractor type * SOA interaction: F(2,14)=5.508, p < 0.05]. We performed separate t-tests on the effect of distractor type for each SOA. Participants were significantly slower when the memory item reappeared in the search task with short and medium SOAs [short: t(7)=5.92, p = 0.001; medium: t(7)=3.44, p < 0.02], but not with the long SOA [t(7)=0.13, p > 0.8]. Thus, the influence of the memorized color on attention indeed decreased over time. This is consistent with the idea that an initial visual representation is converted into a more durable verbal code that then no longer affects visual attention.

4.3 Experiment 2: The time course of more visual working memory effects on attention

In the previous experiment we explored how the influence of presumably more verbal working memory representations on visual attention changes over time.
The time course of working memory effects on visual attention

Figure 4.2: Mean reaction times for each of the distractor types as a function of SOA in Experiment 1. Asterisks indicate significant differences between identical and unrelated distractor conditions as indicated by two-tailed paired t-tests with $p < 0.05$ (*) or $p < 0.01$ (**).

We now explored if and how the influence of more visual working memory changes over time. The only difference to the previous experiment was a memory test that we assumed would require encoding a more visual representation of the to-be-remembered item. Instead of having to distinguish one canonical color from two other canonical colors, participants now had to distinguish one specific shade of a color from two other shades of the same color category. Since observers now presumably had to maintain a more visual representation, we expected more sustained effects on attention.

Methods

Participants

Twenty-seven university students and non-student volunteers ($M = 19.9$ years, range 17 - 24) participated for either 7 Euros or course credit. All reported normal or corrected-to-normal acuity and normal color vision. The data of four participants had to be discarded, because they either performed near chance level on the working memory task (3 participants) or their overall mean search RT was more than four standard deviations above the mean (1 participant).
4.3 Experiment 2: The time course of more visual working memory effects on attention

Apparatus, stimuli, procedure and design

Stimuli, procedure and design were identical to Experiment 1, except that we now presented two variants (different value and / or chroma) of the memorized color in the working memory test along with the to-be-memorized color.

Results and Discussion

Errors on the search task were few and comparable to Experiment 1 (M=3.7%). Performance on the memory task was considerably worse (M=49.4% errors), consistent with the idea that the memory task had become more difficult and observers could not use a verbal label. Table 4.2 provides an overview of the errors. An ANOVA of memory test performance with SOA and distractor type as factors revealed a main effect of SOA [F(2,21)=4.837, p < 0.02]. Participants made fewer errors at the medium SOA (45.7%) than at the short and long SOA (51.3% and 50.5%, respectively). An identical ANOVA of the errors in the search task did not yield any effects.

RTs were analyzed as in Experiment 1. The data trimming method resulted in a loss of 2% of the trials. Figure 4.3 shows the mean reaction times in the identical and unrelated condition as a function of SOA. Participants were slower when the memorized color reappeared in the search task (identical: M=868ms) than when it did not reappear (unrelated: M=843ms) [F(1,22)=6.257, p = 0.02]. Overall reaction times were fastest at the medium SOA and slowest at the short SOA [short: M=872ms, medium: M=833ms, long: M=860ms; F(2,21)=4.007, p < 0.04]. The reaction time difference between search displays with and without reoccurring memory item increased over time [short: M=1ms, medium: M=33ms, long: M=39ms; an interaction that approached significance. F(1,22)=2.696, p = 0.083]. Additional t-tests for each SOA identified significant differences between the identical and unrelated condition for the medium and the long SOAs, but not for the short SOA [short: t(22)=0.07, p > 0.9; medium: t(22)=2.82, p = 0.01; long: t(22)=2.54, p < 0.02]. Finally, we compared Experiment 1 and 2 by conducting an ANOVA with distractor type (identical, unrelated) and SOA (short, medium
4 The time course of working memory effects on visual attention

Figure 4.3: Mean reaction times for each of the distractor types as a function of SOA in Experiment 2. Asterisks indicate differences between identical and unrelated distractor conditions as indicated by significant two-tailed paired t-tests with $p < 0.05$.

...and long) as within-subjects factors and experiment as between-subjects factor. There was no main effect of experiment [$F(1,29)=2.001$, $p = 0.168$]. The three-way interaction of SOA, distractor type and experiment was however significant [$F(2,29)=6.936$, $p < 0.01$], indicating that the influence of more verbal working memory content on visual attention follows a different time course than the influence of more visual working memory content on visual attention.

The absence of an effect of distractor type at the short SOA is somewhat unexpected given the idea that the initial representation is likely to be a visual one (as also suggested by Experiment 1). One possibility is that participants did not bother trying to encode the stimulus given its very brief presentation duration (note that SOAs are blocked). We note that in the same condition of very similar subsequent experiments (Experiment 4 and Experiment 5) there was a memory effect on search. Consistent with a lack of encoding, memory errors in the present experiment were significantly higher than for these later experiments at the short SOA [Experiment 4: 45.5%, $t(29)=1.992$, $p = 0.056$; visual condition of Experiment 5: 46.6%, $t(41)=2.087$, $p < 0.05$]. Participants also made significantly more errors on the memory test at the short SOA (see Table 4.2). Alternatively, the more difficult visual memory task may require a different encoding strategy (i.e. more effortful or attentive processing) which may take some time to initiate. Consistent with this, Soto and Humphreys (2008) also found a delay in memory effects on search when the task load was increased.
4.4 Experiment 3: Preventing verbalization with articulatory suppression

Participants could succeed on the memory test of Experiment 1 by merely remembering the color category of the memory item. Reaction times on the search task indicated that the effect of their working memory content on visual attention decreased with increasing SOA. We speculated that this might be because participants verbalized the to-be-remembered color and that this verbal label did not affect visual attention in the search task when sufficient time had passed between the memory item and the search display. To test if representations were indeed of a more verbal nature in Experiment 1, we prevented verbal coding in the present experiment by adding an articulatory suppression task. As a consequence, participants could not verbalize the to-be-remembered color and had to rely on a visual representation in order to succeed on the memory test at the end of each trial. Furthermore, in Experiment 2 we used a difficult working memory test to make sure that participants would not memorize a verbal label, but encode a visual representation of the to-be-remembered color. We predicted that memory effects on attention would now be sustained and obtained matching results. However, performance on the memory test dropped substantially in comparison to Experiment 1. Thus, the sustained effect we observed could also have been due to the increased memory task difficulty. In the present experiment we induce visual memory through articulatory suppression rather than task difficulty. If the sustained pattern of interference in Experiment 2 is due to the visual nature of the memory content, we should find the same pattern here.

Methods

Participants

Eight university students (between 19 and 25 years old, M=22) participated for either course credit or money. All reported normal or corrected-to-normal acuity and normal color vision.

Apparatus, stimuli, procedure and design

Stimuli, procedure and design were identical to Experiment 1, except that we added an articulatory suppression task. We presented two distinct random numbers between 1 and 9 before the start of each trial which participants continuously articulated until the end of the trial. Each trial now started with the presentation of both numbers (500 ms) in the center of the screen. The memory item was presented after an inter-stimulus-interval of 1500ms. The trial then continued as in Experiment 1. The experimenter was present in the testing room during the experiment to ensure that the participants performed the articulatory suppression task correctly. They all did.

Results and Discussion

Analyses were the same as in Experiment 1. Participants only made a few errors in the search task (5.0%) and on the memory test (6.3%). The respective
4 The time course of working memory effects on visual attention

ANOVAs did not reveal any effects. Table 4.3 shows provides an overview of the errors for each SOA and distractor type. Figure 4.4 shows the mean reaction times for each distractor type as a function of SOA. Data trimming resulted in the loss of 2.3 % of all trials. Participants’ RTs in the search task were slower when the memory item reappeared in the search display [main effect of distractor type: F(1, 7)=59.979, p < 0.001]. The main effect of SOA [F(2,14)=0.990, p > 0.3] and the interaction of SOA and distractor type [F(2,14)=0.148, p > 0.7] were not significant. As is shown in Figure 4.4, memory effects on attention were sustained across SOAs. This was confirmed by separate t-tests [short SOA: t(7)=2.920, p < 0.05; medium SOA: t(7)=2.062, p = 0.078; long SOA: t(7)=3.237, p < 0.05]. We then compared the present experiment to Experiment 2 where we used a difficult memory test instead of articulatory suppression to make participants encode a visual representation of the working memory item. To this end, we performed an ANOVA with SOA (short, medium, long) and distractor type (identical, unrelated) as within-subject factors and experiment (Experiment 2, Experiment 3) as between-subject factor. This only resulted in a marginally significant main effect of experiment, indicating that participants were slower in the search task with articulatory suppression (M=934 ms) than with a more visual representation alone [M=855 ms; F(1,29)=3.426, p = 0.074]. This might be expected on the basis of the additional task demands. An ANOVA on search errors did not reveal any differences between both experiments. An additional ANOVA to compare the present experiment to Experiment 1, i.e. the same experiment, but without articulatory suppression revealed a near significant interaction of SOA, distractor and experiment [F(2,28)=3.454, p = 0.056], suggesting what is already apparent from the figures, namely that the time courses differed for these experiments. An analogous ANOVA comparing the search accuracies of both experiments did not reveal any effects. These results indicate that we successfully induced a visual working memory representation by articulatory suppression, resulting in a sustained effect of visual working memory content on attention. Thus, we can conclude that a) the resulting memory representation in Experiment 1 was indeed of a more verbal nature; b) the sustained pattern of

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<th>SOA (ms)</th>
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<tr>
<td>identical</td>
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<td>6.7%</td>
<td>5.4%</td>
</tr>
<tr>
<td>unrelated</td>
<td>7.1%</td>
<td>5.4%</td>
<td>5.4%</td>
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Table 4.3: Error percentages for the search and memory tasks in Experiment 3 as a function of SOA and similarity of the visual distractor to the memory item.
4.5 Experiment 4: Limiting visual encoding by an additional visual task

Given the difficulty participants had with the visual memory test in Experiment 2, it is likely that the creation of a more sustained visual memory representation requires effort, i.e. attention to the memory item. If we limit the amount of time that the stimulus can be attended, we should also limit the strength of the memory representation and its influences should be less sustained. In the present experiment, we added a rapid serial visual presentation (rsvp) stream of small letters onto the memory item after it had been presented for 100 ms. The rsvp stream informed participants whether or not they had to perform the search task by occasionally containing the letter ‘X’ (go-nogo task). Participants were instructed to monitor the rsvp stream and to withhold their response in the search task whenever the ‘X’ had been part of the stream. If the duration of encoding is an important factor in how visual memory affects attention, then we may expect a decrease in memory effects on search here.

Figure 4.4: Mean reaction times for each of the distractor types as a function of SOA for the verbal memory type while participants performed an articulatory suppression task in Experiment 3. Asterisks indicate significant differences between identical and unrelated distractor conditions as indicated by two-tailed paired t-tests with \( p < 0.05 \). The difference marked ‘x’ is only significant under a one-tailed t-test.

Experiment 2 was due to the more visual nature of the memory task, not due to the task difficulty per se; and c) the time course of verbal and visual working memory effects on attention are indeed different.

4.5 Experiment 4: Limiting visual encoding by an additional visual task
Methods

Participants

Ten university students participated for either course credit or money. They were between 18 and 23 years old (M=20). The data of two participants had to be discarded, because they failed to comply with the task instructions. They did not withhold their response on the large majority of nogo trials (81% and 69%).

Apparatus, stimuli, procedure and design

Stimuli, procedure and design were identical to Experiment 2, except that we additionally asked participants to monitor an rsvp stream of letters presented on top of the memory item. On each trial, the memory item was initially presented for 100 ms, followed by the presentation of a small letter in the center of the screen, i.e. on top of the memory item for 50 ms. This sequence was continued during the whole presentation duration of the to-be-remembered color (150 ms, 500 ms or 1000 ms). Letters were chosen randomly from all letters of the alphabet, excluding the letters ‘M’ and ‘N’. The letter ‘X’ was included in the stream on four trials per block. On these trials, participants were asked to withhold their response in the search task.

Results and Discussion

We analyzed the data as in Experiment 1. Participants made very few errors on the search task (3.5%), but many errors on the memory test (43.2%), as before. Participants improved on the search task with increasing SOA [main effect of SOA: F(2,18)=6.096, p<0.05]. An ANOVA on errors on the memory task did not reveal any effects. Table 4.4 shows the error percentages on the search task and memory test for each SOA and distractor type. Figure 4.5 shows the search RTs for both distractor types as a function of SOA. Data trimming resulted in the loss of 2.5% of all trials. Reaction times decreased with increasing SOAs [main effect of SOA: F(2,14)= 7.693, p < 0.05]. Participants’ reaction times were slower when

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Table 4.4: Error percentages for the search and memory tasks in Experiment 4 as a function of SOA and similarity of the visual distractor to the memory item.
4.5 Experiment 4: Limiting visual encoding by an additional visual task

the memory item reoccurred in the search display [main effect of distractor type: F(1,7)=19.194, p < 0.01]. This effect decreased with increasing SOA [interaction of SOA and distractor type: F(2,14)= 4.438, p < 0.05; short SOA: t(7)=4.527, p < 0.01; medium SOA: t(7)=3.815, p > 0.01; long SOA: t(7)=0.973, p > 0.3]. Thus, the time course appeared to differ from that found in Experiment 2. An

![Figure 4.5: Mean reaction times in Experiment 4 for each of the distractor types as a function of SOA for the visual memory type while participants additionally monitored a stream of letters. Asterisks indicate significant differences between identical and unrelated distractor conditions as indicated by two-tailed paired t-tests with p < 0.01.](image)

ANOVA with the factors SOA (short, medium, long) and distractor type (identical, unrelated) as within-subject factors and experiment (Experiment 2, Experiment 4) as between-subject factor confirmed this. It showed that search was overall slower in Experiment 4 (M=1004 ms) than in Experiment 2 [M=855 ms; main effect of experiment: F(1,29)=15.134, p < 0.01]. This is expected, given the additional task demands. The effect of the reappearing memory item was overall more pronounced in Experiment 4 (M=76 ms) than in Experiment 2 [M=24 ms; interaction of distractor type and experiment: F(1,29)=7.357, p < 0.05]. Most importantly, adding an additional visual task onto the memory item changed the time course of visual working memory effects on attention from sustained to decreasing with increasing SOA [interaction of SOA, distractor type and experiment: F(2,58)=7.130, p < 0.01]. These results support the idea that a visual memory representation only affects attention in a sustained manner when there is enough time to encode the visual stimulus.
4.6 Experiment 5: Limiting processing time by reducing cue duration

In Experiment 4, we limited the encoding time of the to-be-remembered color by presenting an additional visual task during presentation of the memory stimulus. Reducing the presentation duration of the memory cue to the same brief time span at all SOAs should also limit the time that observers can attend to and encode the visual stimulus. This should then yield the same pattern as in the previous experiment, i.e. a decrease of visual working memory effects on attention with increasing SOA. Thus in Experiment 5, we used a constant cue duration of 150 ms and varied the ISI such that the overall SOA remained identical to the previous experiments. This manipulation should not affect how easily verbalizable working memory content affects attention over time, since more verbal representations should not depend on the actual duration of the visual stimulus (as long as it is clearly visible in the first place).

Methods

Participants

Twenty-three university students aged 18 to 44 years (Mean= 22) participated for course credit or money. They all reported having normal or corrected to normal acuity and color vision. The data of three participants were excluded from the analysis, because they made more than 10% errors in the search task (2 participants) or they performed near chance level on the memory test (1 participant).

Apparatus, stimuli, procedure and design

Apparatus, stimuli, procedure and design were identical to Experiment 1 (for the more verbal memory type) and Experiment 2 (for the more visual memory type), except that the SOA now always consisted of a fixed cue duration (150 ms) and a variable ISI (150 ms, 850 ms, 3350 ms). The overall SOAs remained identical to the previous experiments. We used a within-subject design. Half of the participants started with the verbal memory type, the other half with the visual memory type. After a short break, the participants continued with the verbal memory type, if they had started with the visual memory type and vice versa.

Results and Discussion

Overall, participants made few errors on the search task (M=3.4%; verbal working memory content: M=3.3%, visual working memory content: 3.8%). Table 4.5 shows the error percentages for each condition and SOA, separately for each memory type. Participants performed worse on the memory test for the visual memory content (M=48.1% errors) than for the verbal memory content (M=2.8% errors), consistent with the idea that observers could not use a clear verbal or semantic label. We did not find any significant effects of either SOA, distractor type, memory type or an interaction of these factors in
4.7 General Discussion

In five experiments, we investigated the time course of the influence of working memory content on visual attention. We found that the influence of more verbal working memory content on visual attention decreased with increasing SOA (Experiments 1 and 5). The influence of more visual working memory content on visual attention was sustained whenever participants had enough time to attend to and encode the memory item (Experiment 2 and 3). When processing time was limited by either an additional visual task during encoding or by a brief presentation duration of the memory item, the effect of visual working

the search task. Participants made more errors on the memory test with visual working memory content (M=48%) than with verbal working memory content (M=2.7%) [F(1,19)=717.639, p < 0.001], they made more errors after the long SOA (M=28.1%) than after the short and medium SOAs (M=24.3% and M=23.9%, respectively) [F(2,38)=4.932, p < 0.05]. Participants made fewer memory test errors when the memory item reappeared in the search display (M=24.4%) than when it did not (M=26.4%) [F(1,19)=5,752, p < 0.05]. This difference was only significant for the visual memory type [identical: 46.4%, unrelated: 49.9%, t(19)=2.438, p < 0.05], but not for the verbal memory type [identical: 2.6%, unrelated: 2.9%, t(19)=0.655, p > 0.5], leading to a memory type x distractor type interaction [F(1,19)=6.244, p < 0.05].

The trimming of RT data resulted in the loss of 2.2% of all trials. Figures 4.6(a) and 4.6(b) depict the mean RTs for each of the distractor types as a function of SOA for the verbal and visual working memory content, respectively. Overall, participants searched faster with verbal working memory content (M=860 ms), than with visual working memory content (M=897 ms) [Main effect of memory type: F(1,19)=4.046, p = 0.058]. Participants were slower when the memory item reappeared in the search display (identical: M=901 ms) than when it did not reappear (unrelated: M=855 ms) [F(1,19)=33.030, p < 0.001]. Overall, this effect of working memory decreased with increasing SOA (short: M=63 ms, medium: M=53 ms, long: M= 21 ms) [SOA*distractor type interaction: F(2,38)=4.607, p < 0.05]. The three-way interaction of memory type, SOA and distractor type was not significant [F(2,38)=0.465, p > 0.6], indicating that the time courses of both memory types did not differ. Separate t-tests comparing the effect of distractor type for each SOA and memory type showed that participants’ RTs were slower when the working memory item reoccurred in the search task at the short and medium SOA, but not at the long SOA. This was the case for both memory types [more verbal 300 ms: t(19)=3.405, p < 0.01; more verbal 1000 ms: t(19)=4.321, p < 0.001; more verbal 3500 ms: t(19)=1.320, p > 0.2; more visual 300 ms: t(19)=4.563, p < 0.001; more visual 1000 ms: t(19)=2.813, p < 0.05; more visual 3500 ms: t(19)=1.159, p > 0.2]. Thus, the effect of verbal as well as visual working memory content decreased with increasing SOA. Apparently, decreasing the duration of the to-be-memorized stimulus is another way to change a sustained visual memory effect on attention into a decreasing one. As expected, the time course of verbal working memory effects was not affected by this manipulation.

4.7 General Discussion

In five experiments, we investigated the time course of the influence of working memory content on visual attention. We found that the influence of more verbal working memory content on visual attention decreased with increasing SOA (Experiments 1 and 5). The influence of more visual working memory content on visual attention was sustained whenever participants had enough time to attend to and encode the memory item (Experiment 2 and 3). When processing time was limited by either an additional visual task during encoding or by a brief presentation duration of the memory item, the effect of visual working memory content decreased with increasing SOA. Apparently, decreasing the duration of the to-be-memorized stimulus is another way to change a sustained visual memory effect on attention into a decreasing one. As expected, the time course of verbal working memory effects was not affected by this manipulation.
4 The time course of working memory effects on visual attention

(a) Verbal working memory content

(b) Visual working memory content

Figure 4.6: Mean reaction times for each of the distractor types as a function of SOA in Experiment 5. Asterisks indicate significant differences between identical and unrelated distractor conditions as indicated by two-tailed paired t-tests with \( p < 0.05 \) (*) or \( p < 0.01 \) (**).
memory content also decreased over time (Experiments 4 and 5). Thus, working memory content differentially interfered with visual attention as a function of time, depending the type of working memory content and visual processing duration. The study is the first to fully explore the time course of memory-based interference in visual attention, and resolves an apparent empirical discrepancy between a few previous studies, some of which did show an effect of easily verbalizable working memory material on attention, and some of which did not. Related studies have addressed the influence of different types of working memory content on attention (e.g. Soto & Humphreys, 2007; Olivers et al., 2006; Houtkamp & Roelfsema, 2006; Downing & Dodds, 2004). However, they usually either focused on global questions (i.e. Does working memory at all interfere with attention?) or on the question whether memory effects on attention are automatic or controlled. The latter commonly tends to be presented as a dichotomy (i.e. involuntary "capture" vs. flexible use of working memory; e.g. Olivers et al. 2006; Woodman & Luck 2007). So far, only Soto and Humphreys (2008) previously asked if the time between the to-be-memorized item and the search display played a role in the interaction of working memory and attention. Although they did not include the full range of SOAs and stimulus durations used here, their results are largely consistent with ours. When memory items were verbalizable, a clear effect on attention was found for SOAs up to approxi-

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Table 4.5: Error percentages for the search and memory tasks for each memory type in Experiment 5 as a function of SOA and similarity of the visual distractor to the memory item.
4 The time course of working memory effects on visual attention

mately 1000ms. They did not test beyond 1000ms, leading them to conclude that there was no effect of SOA. Incorporating a wider range of SOAs, however, our study does suggest a decrement in memory-based effects with more time between the memory item and the search display. When verbalization was made difficult (in their case through articulatory suppression), Soto and Humphreys (2008) found that memory effects occurred for the later SOAs, but not for the earliest SOA. This is directly consistent with the present results of Experiment 2, which showed a similar time course when colors were made difficult to distinguish.

In order to investigate whether the memory-based benefits found by Woodman and Luck (2007) were due to the timing-parameters they used, we included their cue duration (500 ms) and ISI (500 ms). We again found memory-based interference instead of benefits, suggesting that the discrepancy is not a result of the time between the memory item and the search display. A recent study by Han and Kim (2009) does suggest a role for time here, be it the time into the search task. They found that memory-matching distractors result in increased interference shortly after the onset of the search display, whereas later on they may yield benefits. This suggests the operation of cognitive control processes that needs time to be implemented.

At first sight, memory effects on attention after an SOA of several seconds seem to contradict to the findings of Downing and Dodds (2004) and Houtkamp and Roelfsema (2006). Both used cue durations and ISIs in the range of seconds and used articulatory suppression to promote visual memory. Nevertheless they found either no interference of working memory on attention, or even a benefit (Experiment 2 of Downing and Dodds, 2004). However, these studies differ in many ways from the experiments reported here. The most important cause of a lack of memory effect in their studies is probably the fact that their search target changed from trial to trial. This meant that on every trial, participants not only had to remember the memory item, but also the search target. Olivers (2009) has shown that having to additionally remember the search target considerably reduces the influence of the irrelevant memory item on search reaction times (see also Oh & Kim, 2003). In the present experiments, we only presented one memory item on each trial and kept the target constant across all experiments and conditions. This resulted in a decreasing effect of working memory on attention when the memory item was easy to verbalize and a sustained effect of working memory on attention when the memory item was difficult to verbalize.

What causes this difference in time course? A possible explanation is that each item is first encoded visually and can then easily interfere with visual attention, since both are of the same type. The more time passes between the to-be-remembered item and the search display, the more time there is to transform the easy to verbalize visual representation into a verbal representation. The verbal representation can then no longer interfere with visual attention. Thus, the traditional notion that working memory contains separate subsystems for verbal and visual content which selectively interfere with verbal and visual attention respectively, still has merit. When the memory cue is difficult to categorize or a visual representation is induced by articulatory suppression, interference with
4.7 General Discussion

visual attention seems to be sustained, provided that the item is presented sufficiently long to allow the creation of a sufficiently strong visual representation. In any case, the present study shows that some differential empirical results in the recent literature on working memory effects on attention can be explained in terms of the time course of such effects.
The costs of switching attentional sets

People prioritize those aspects of the visual environment that match their attentional set. In the present study, we investigated whether switching from one attentional set to another is associated with a cost. We asked observers to sequentially saccade towards two color-defined targets, one on the left side of the display, the other on the right, each among a set of heterogeneously colored distractors. The targets were of the same color (no attentional set switch required) or of different colors (switch of attentional sets necessary), with each color consistently tied to a side, to allow observers to maximally prepare for the switch. We found that saccades were less accurate and slower in the switch condition than in the no-switch condition. Further, whenever one of the distractors had the color associated with the other attentional set, a substantial proportion of saccades did not end on the target, but on this distractor. A time course analysis revealed that this distractor preference turned into a target preference after about 250 - 300 ms, suggesting that this is the time required to switch attentional sets.

5 The costs of switching attentional sets

5.1 Introduction

Whenever people look for an object, they prioritize those aspects of the visual environment that match their attentional set. This set is thought to represent a target-defining feature, for instance the object’s color. It biases the visual system such that attention is guided towards the target object (e.g. Olivers & Eimer, 2010; Wolfe & Horowitz, 2004). Is there a cost associated with switching from one attentional set to another?

There is a large body of literature showing that switching from one task to another is associated with costs (Jersild, 1927; Monsell, 2003). However, task switching does not only involve a switch in attentional sets, but typically also a switch in response categories (Rushworth, Passingham, & Nobre, 2005). The aim of the present study is to investigate the costs of a purely attentional switch rather than a complete task switch.

Several previous studies have used a cueing procedure to address this issue. For example Vickery, King, & Jiang (2005) presented observers with a visual search task that was preceded by a cue indicating the target on each trial. Search became slower with decreasing stimulus-onset-asynchrony (SOA), suggesting that observers needed time to implement the new attentional set. However, this time interval may at least partly reflect the time needed to process the cue and not an attentional switch cost. Vickery et al. (2005) always changed the target from trial to trial and thus did not have a baseline allowing the comparison between switch and no-switch trials. Wolfe (2004) employed a similar procedure in which observers looked for a cued target. Again, search improved with more time between the cue and the search display. This study did include a baseline condition. In this condition, target identity was blocked, such that both the target and the cue were always the same from trial to trial. However, note that this then eliminates the need to process the cue in the baseline condition, which again raises the possibility that the reaction time costs observed in the other conditions reflect the cue processing time instead of switch costs. Another study, by Rushworth et al. (2005), directly compared cues instructing observers to switch attentional sets to cues instructing to maintain the current set in a mixed design. This way, both types of cue had to be processed. They found target response times to be slowed by only about 10 ms after a switch cue, suggesting that attentional switch costs may only be marginal. However, the time between the cue and the target display was fixed at 2000 ms, allowing for ample time to prepare. Accordingly, the small effect might therefore represent an underestimation.

Performance costs are apparent when people are asked to look for two targets at the same time relative to looking for only one target (Houtkamp & Roelfsema, 2009; Menneer, Cave, & Donnelly, 2009; Moore & Osman, 1993). Even though this suggests that it is difficult to maintain two attentional sets at the same time, this does not directly demonstrate that there is a cost of switching between them. In fact, Adamo and colleagues (Adamo, Pun, Pratt, & Ferber, 2008; Adamo, Wozny, Pratt, & Ferber, 2010b; Adamo, Pun, & Ferber, 2010a) recently proposed that two attentional sets can even be used simultaneously, as long as each feature set is tied to a specific location, e.g. green to the left and
red to the right side of the display’s center. Adamo et al. (2008) first presented a placeholder box on each side of a fixation cross. After a brief delay, a color cue appeared around one of the placeholders, followed by the presentation of a target in one of the placeholder boxes. Participants were asked to respond only to targets of one color (e.g. blue) on one side (e.g. left) and to targets of the other color (e.g. green) on the other side (e.g. right) and to refrain from responding in all other cases. They found a cueing benefit relative to target only presentations when a matching color cue was presented at the matching location (e.g. green cue and green target on the right), but not when a non-matching color cue was presented. This suggests that two attentional control sets can be maintained simultaneously as long as both sets are tied to separate locations in space. If observers are indeed able to maintain two spatially separated attentional sets in parallel, one might expect the costs of switching between these sets to be minimal.

The present study directly investigates the cost associated with switching attentional sets. We conducted two experiments in which observers were presented with displays consisting of four circles of different colors on the left side of fixation, and another four colored circles on the right side. There was a target circle on each side. The task of the observers was to make a saccade first to the left target, and then to the right target, as fast as possible. To prevent the pre-programming of saccades, the two halves of the display were presented sequentially, with the second display appearing as soon as observers looked at the first target. Crucially, the target was either of the same color on both sides (e.g. both red; the no-switch condition), or of different colors (e.g. red on the left, green on the right; the switch condition). In both conditions, the target colors were pre-specified for an entire block, and importantly, in the switch condition, each target color was consistently tied to a location. By always presenting the two target displays in the same order, and consistently tying them to the same location, we sought to enable observers to simultaneously maintain both sets (Adamo et al., 2008) and thus prevent switch costs, if possible. The rationale is that if even under these optimal circumstances performance suffers, then we can conclude that switching attentional sets comes at a cost. Experiment 1 indeed shows such costs when a switch in feature set is required. Experiment 2 further explores this cost by having each target accompanied by a distractor matching the opposite set. While attention has not yet fully switched, observers should be more distracted by an object matching the current set. This allowed us to measure the time course of switching.

5.2 Experiment 1

There were two main conditions. In the no-switch condition, observers had to saccade towards targets of the same color presented on the left (T1) and on the right (T2) side of the display (e.g. with both targets being red). In the switch condition, observers had to saccade towards a target of one color on the left side (T1; e.g. green), but another color (T2; e.g. red) on the right side of the display. Target colors remained constant within one block of trials. The second target
The costs of switching attentional sets

display only appeared after observers had selected the first target. We asked our participants to make a fast and direct saccade to the targets as soon as the display appeared on the screen.

If switching attentional sets is associated with costs despite the fact that the different targets are consistently tied to distinct display sides, saccades from one to the other color target should be less accurate or slower than when the targets have the same color.

In order to control for direct priming from one target to the next, we also included conditions in which only the second target would appear (the T2 only condition). For example, in the standard case, a green target might appear on the left, followed by another green target on the right. It has been shown that such target repetitions lead to faster performance due to priming (Maljkovic & Nakayama, 1994; Olivers & Humphreys, 2003). On T2 only trials, only the right green target would appear. If there is still an advantage relative to the switch condition, then this must be due to the fact that there is no need to switch sets rather than due to priming.

Methods

Participants and Apparatus

Sixteen university students participated for either course credit or money. The stimuli were generated using a standard PC running E-Prime (version 1.2; Psychology Software Tools, Pittsburgh, PA) on a 19” color monitor at 100 Hz. Viewing distance was about 65 cm. Eye movements were recorded with an Eyelink 1000 eye tracker (SR research) using the standard built-in saccade detection algorithm. Data were analyzed with Matlab (Mathworks, Natick, MA).

Design, Stimuli and Procedure

Figure 5.1 shows a schematic depiction of one trial of the switch condition with the first saccade target (T1) on the left side and the second saccade target (T2) on the right side of the display. In the no-switch condition, both T1 and T2 had the same color. In the switch condition T1 and T2 were differently colored. Each trial started with the presentation of a fixation cross in the center of the screen (until stable fixation of at least 1 second). Drift correction was performed during the presentation of the fixation cross. Then, the outlines of four circles were presented on each side of the screen, equidistant from fixation (about 7 degrees). After a further 500 ms of stable fixation, the circle outlines on one side were filled with color. There were always three distractor colors (blue, yellow, gray; CIE x,y coordinates 0.211, 0.177; 0.417, 0.484; 0.303, 0.333) and one target color (red or green; CIE x,y coordinates 0.572, 0.343; 0.304, 0.509). We did not attempt to equate all colors for luminance, but we chose the target colors such that they were not the brightest nor the dimmest. In addition, the two target colors were counterbalanced within subjects. On half of all trials, the first display half was presented consisting of four colored circles, one corresponding to T1. After the eyes landed on this target, the second half was presented at the opposite side of
5.2 Experiment 1

fixation and the first half disappeared. The second display half always consisted of T2 and three distractors. If T1 was not reached after 800 ms, an error message was shown on the screen for one second and the trial was started again. On the other half of the trials, the side that contained T2 appeared first, requiring participants to make a saccade to T2 only (see lower panel in Figure 5.1). This manipulation was included to exclude the possibility that the color of T1 directly primed the color of T2 in the no-switch condition and to force participants to keep two sets active in the switch condition. If they did not look at T2 within 800 ms, an error message was shown on the screen and a new trial was started.

Each participant completed 4 blocks of 100 trials with the color combinations red-red, red-green, green-red and green-green for T1 and T2, respectively. The order of blocks was counterbalanced across participants. Whenever participants were asked to make two fast successive eye movements (first to T1, then to T2), T2 appeared together with three distractors as soon as participants looked at T1. At the same time, T1 and the first three distractors disappeared. For half of the participants the side containing T1 was always presented on the left side of the display, requiring a leftward saccade to T1 followed by a rightward saccade to T2 or only one rightward saccade to T2. For the other half of the participants, this assignment was reversed. T1 and T2 were always randomly placed on one of the four possible positions within a display half. Participants completed 20 practice trials.

Data analysis

We discarded saccades with latencies below 80 ms and above 600 ms and trials with blinks or other artifacts (in total 35% of all saccades were excluded). Note that since observers had to perform two eye movement tasks (one on the left and one on the right), the chance of an error was increased. Saccades were defined as having ended on a target or a distractor circle when the endpoint of the saccade fell into a ‘wedge’ shaped region around the circle with an inner radius of about 6.5 degrees and an outer radius of about 10.5 degrees from the center of the screen. We focused our analysis on three saccade types: A) the first saccade after T1 onset that ended either on the target or on one of the distractors, B) the first saccade after T2 onset that ended either on the target or on one of the distractors in trials when only T2 was presented and C) the first saccade after T2 onset, which ended either on T2 or one of the distractors in trials in which T1 had been presented (and was looked at) first. We calculated the proportion of saccades to the target relative to all saccades that ended on any object (target or distractor) and the time to the target, i.e. the time between display onset and the end of the saccade for each of these saccade types.

Results and Discussion

Figure 5.2 shows the proportion of saccades that ended on a target in each of the conditions and for each saccade type. An ANOVA with the factors condition (no-switch, switch) and saccade type (T1, T2 only, T2 after T1) revealed an overall drop in accuracy of 9.3% whenever participants had to switch between
The costs of switching attentional sets

attentional sets (main effect of condition: $F(1, 15) = 39.280, p < 0.001$). Further, there was an accuracy difference between saccade types (main effect of saccade type: $F(1, 15) = 30.245, p < 0.001$). Saccades to T2 after T1 were less accurate (Mean saccades to target = 61.2%) than saccades to T2 only (Mean saccades to target = 82.4%) and to T1 (Mean saccades to target = 82%). The interaction of condition and saccade type was not significant. Nevertheless, we tested if the drop in accuracy for the switch condition relative to the no-switch condition was significant for each saccade type. This was indeed the case. Accuracy was on average 6% lower in the switch condition than in the no-switch condition for saccades to T1 ($t(15) = 2.885, p < 0.05$), 11% lower for saccades to T2 only ($t(15) = 4.957, p < 0.001$), and also 11% lower for saccades to T2 after T1 ($t(15) = 3.309, p < 0.01$).

An ANOVA with the same factors on the time to target revealed that participants were on average 9 ms slower whenever they had to switch attentional sets (main effect of condition: $F(1, 15) = 8.576, p = 0.01$). This difference was most pronounced for saccades to T2 only (18 ms), whereas it was less pronounced for saccades to T2 after T1 was presented (4 ms) and for saccades to T1 (4 ms, interaction of condition with saccade type: $F(2, 30) = 7.41, p < 0.01$). These
results go against the hypothesis that switching can be performed without any costs. Even though both sets were consistently tied to separate spatial locations, performance was worse in the switch than in the no-switch condition.

5.3 Experiment 2

In Experiment 1 we used displays consisting of multiple heterogeneous objects for two reasons. First, we wanted to encourage participants to adopt feature-specific attentional sets, and second, we wanted to see if they would adopt a separate set for each side of the display, because previous work suggested that two sets may be maintained in parallel under these circumstances (Adamo et al., 2008). However, note that it was not strictly necessary to tie the two different target colors to specific sides of the display to do the task. Participants could decide to just look for any of the target colors anywhere in the display (i.e. adopt a pair of display-wide sets rather than location-specific sets). After all, the T1 and T2 displays each contained only one object that matched one of the sets (i.e. the targets), thus automatically leading to selection. It is possible that having to switch between multiple display-wide sets is costly, while switching sets between two different spatial areas is efficient.

Experiment 2 was designed to prevent display-wide attentional settings, and to further coerce observers to prepare for the attentional switch. We did this by including the other target color as a distractor in each of the display halves. Thus, if the task was to look for red on the left and green on the right, a green distractor was present on the left, and a red distractor on the right. This way
participants should have every incentive to look for only one particular color at only one particular side of the screen. If switching location-specific sets is associated with switch costs, we should again find costs for the condition requiring two sets compared to the condition that required only one set. Moreover, we then expected that the distractors associated with the other attentional set would interfere with search by attracting attention. A second advantage of this procedure is that we can assess the time course of the attentional switch by looking at the accuracy of the eye movements to the second display as a function of time since display onset. Early in time observers may still be employing the old attentional set and thus look at the matching distractor more often than at the new target. With time, however, observers will have switched attentional sets and thus prefer the target. The crossover of these preferences can then be taken as the switch time.

Methods

The present experiment was identical to Experiment 1, except that now both possible target colors (red and green) always appeared together with two distractors (blue and yellow) on each side of the search display. Thus, the gray distractor of the previous experiment was replaced by the color associated with the other attentional set. In the no-switch condition, the gray distractor was replaced with the other, now irrelevant, possible target color. Sixteen university students received either course credit or money for participating in the experiment. In total, 24% of all saccades needed to be discarded due to blinks and other artifacts.

Results and Discussion

Figure 5.3 shows the proportion of saccades that went to the target and to the distractor associated with the other attentional set for each saccade type and condition. We found an overall drop in accuracy of 26.3% when participants had to switch attentional sets (main effect of condition: F(1, 15) = 191.740, p < 0.001). Overall accuracy was lowest for saccades to T2 after T1 (38.1%), intermediate for saccades to T2 only (53.1%) and highest for saccades to T1 (66.7%, main effect of saccade type: F(1, 15) = 61.619, p < 0.001). The differences in accuracy between conditions varied with saccade type (interaction of condition with saccade type: F(2, 30) = 6.457, p < 0.01). In the switch condition, accuracy was on average 22 % lower than in the no-switch condition for saccades to T1 (t(15) = 6.666, p < 0.001), 21 % lower for saccades to T2 only (t(15) = 12.656, p < 0.001) and 35 % to T2 after a saccade to T1 (t(15) = 6.439, p < 0.001).

In addition, we found an overall cost in the time to target of on average 21 ms whenever participants were supposed to switch attentional sets (main effect of condition: F(1, 15) = 8.991, p < 0.01). Further, the time to T2 after presentation of T1 was overall fastest (243 ms), the time to T2 only was intermediate (255 ms), whereas the time to T1 was slowest (262 ms, main effect of saccade type: F(1, 15) = 3.409, p < 0.05). The difference in time to target between the switch condition and the no-switch condition was most pronounced for saccades to T2 only (33
5.4 General Discussion

In two experiments, we assessed whether people can efficiently switch attentional sets. We asked observers to sequentially saccade towards two targets of the same color (no-switch condition) or of different colors (switch condition), ms), intermediate for saccades to T1 (17 ms) and smallest for saccades to T2 after the presentation of T1 (15 ms, interaction of condition with saccade type: F(2, 30) = 3.409, p < 0.05).

For each type of saccade we then compared the proportion of saccades that erroneously ended on the distractor associated with the other attentional set to the proportions expected to end on this distractor if there would be no interference from the other set. To do so, we computed the average proportion of saccades that ended on a regular distractor (blue and yellow). If the distractor that was associated with the other attentional set was treated as a regular distractor, a similar proportion of saccades should have ended on this distractor. These proportions are indicated as dotted lines in Figure 5.3. However, we found that whenever participants were supposed to switch attentional sets, significantly more saccades went to the distractor associated with the other set than to a regular distractor. These differences were 16% for saccades towards T1 (t(15) = 7.995, p < 0.001), 34% for saccades towards T2 only (t(15) = 10.313, p < 0.001), and 14% for saccades towards T2 after T1 was presented (t(15) = 4.627, p < 0.001). In the no-switch condition the proportion of saccades that ended on the now irrelevant distractor was about equal to the expected proportion (see Figure 5.3, all t(5) < 1.964, all p > 0.06). If anything, there was a trend towards a suppression of the irrelevant distractor.

To estimate the switch time, we analyzed saccadic accuracy for T2 as a function of time (since T2 onset, cf: van Zoest, Donk, & Theeuwes, 2004). For this purpose, we binned the first two saccades into six bins and determined the average time to the target and the proportion of saccades that ended on T2, as well as the proportion of saccades that ended on the distractor associated with the other set. Figure 5.4 depicts the proportion of saccades that ended on the target (solid lines) and on the distractor associated with the other attentional set (dashed lines) as a function of time to target. Whenever participants did not need to switch, already the majority of even the fastest saccades ended on the target. The more time passed, the higher the proportion of saccades that were correctly directed to the target. However, when participants had to switch attentional sets, the earliest saccades ended on the distractor associated with the first set. This indicates that participants were still using the first (i.e. old) attentional set (Folk, Remington, & Johnston, 1992; Al-Aidroos & Pratt, 2010). The proportion of correct saccades to the target (i.e. second set) then gradually increased, while the proportion of saccades to the distractor associated with the other (i.e. first) attentional set gradually decreased. As shown in Figure 5.4, the competition between the old-set distractor and new-set target shifted balance in favor of the latter around 250-300 ms post onset, suggesting that this is the time it takes to switch.
5 The costs of switching attentional sets

Figure 5.3: Proportion of saccades to the target (T) and the distractor associated with the other set (D) in Experiment 2. Dotted lines indicate the average proportion of saccades that ended on a regular (blue or yellow) distractor.

corresponding to either one display wide attentional set, or to two attentional sets tied to different parts of the display. Each target was always presented together with three differently colored distractors, in order to ensure that selection had to be based on the feature associated with the attentional set (i.e. color). We found that saccades in the switch condition were slower, and especially less accurate than in the no-switch condition. Further, we found that whenever a target was presented together with a distractor having the color associated with the other attentional set, a large proportion of saccades did not end on the target, but on this distractor. This interference clearly speaks against the possibility that attentional switches can be performed without any costs. This was further supported by an analysis of the time to target for saccades towards the second target showing that participants shifted from the first (i.e. old) to the second (i.e. new) set about 250 ms to 300 ms after T2 onset.

Our study shows that a switch between attentional sets is associated with costs, even when these sets are tied to separate spatial locations. Adamo et al. (2008) suggested that attentional sets could be maintained simultaneously as long as these sets refer to separate spatial locations. Our results do not exclude the possibility that people can simultaneously maintain two attentional sets to at least some extent (see also Ansorge & Heumann, 2004; Ansorge, Horstmann, & Carbon, 2005; Ansorge & Horstmann, 2007). However, our results suggest that if people have this ability, this does not preclude the occurrence of switch costs. Indeed, recently, Moore and Weissman (2010; 2011) have proposed that it is pos-
Figure 5.4: Proportion of saccades from T1 to T2 that ended on the target (solid lines) and on the distractor associated with the other attentional set (dashed lines) as a function of time to target.

Possible to passively keep two attentional sets in memory, but for a set to affect selection, it needs to be put in the active focus of attention (see also Adamo, Wozny, Pratt, & Ferber, 2010b; Parrott, Levinthal, & Franconeri, 2010, for a similar view). It is quite possible that the switch costs we find reflect this process. Our study provides a more direct assessment of attentional switch costs than previous studies that have used cues to indicate a new target on each trial. Those studies came also to the conclusion that it takes time to change the target set. However, such estimates invariably include the time it takes to interpret the cue and not only the time to perform the switch. Moreover, as Wolfe (2004) showed, these estimates depend on the type of cue used, with picture cues causing optimal performance at a 200 ms cue-target SOA, while word cues need more than 800 ms. The only study that controlled for cue processing time between switch and no-switch trials is Rushworth et al. (2005). However, in that study, only a single SOA of 2000 ms was used, precluding the possibility to estimate the switch time.

Our findings are completely in line with the literature on task switching (Jersild, 1927). In task switching experiments, participants are asked to apply two different stimulus-response rules to the same perceptual stimulus (see e.g. Allport, Styles, & Hsieh, 1994). Usually, participants are less accurate and slower in responding to the stimulus when they switch stimulus-response rules from trial to trial than when they apply the same rule on two consecutive trials. This is even the case when the switch is completely predictable (e.g. on each trial, or on
every second trial) and each stimulus-response rule is tied to specific location in the display, as shown by Rogers & Monsell (1995). These authors estimated the switch cost for such predictable switching to be between 200 and 300 ms, which is consistent with the estimate of 250 - 300 ms we obtained. It is also consistent with estimates of what has been termed the "attentional dwell time" in paradigms where observers need to switch from identifying a digit to identifying a letter (Duncan, Ward, & Shapiro, 1994; Ward, Duncan, & Shapiro, 1996). Our results also agree nicely with findings by Moore and Weissman (Moore & Weissman, 2011, 2010). Their participants looked for targets in either of two possible colors in a central RSVP stream flanked by two peripheral streams. They found that 100 - 300 ms after a target colored distractor had been presented in a peripheral stream, it was more difficult to identify a differently colored target, because the first attentional set was still active ('in the focus of attention'). Taken together, these and our results show that people need some time to switch between two tasks or between two attentional sets, and that this takes about a quarter of a second.
Summary / Samenvatting

The visual environment contains a vast amount of information, most of which is irrelevant for our current goals. Still, we need to be able to select those parts that are necessary to act purposefully. This means that the brain faces the difficult task of extracting relevant and discarding irrelevant information. It accomplishes this using a mechanism called selective attention. Selective attention prioritizes some stimuli in the visual field over others, such that they are processed with more resources. Selective attention is assumed to be controlled by two mechanisms: a bottom-up mechanism and a top-down mechanism. Bottom-up selection is stimulus-driven: the bottom-up mechanism prioritizes stimuli that are salient relative to their local surroundings. These stimuli might, for example, have a unique color or orientation, move among static surrounding elements, or differ in size relative to the other stimuli. Top-down selection is goal-driven: the top-down mechanism prioritizes stimuli that are in line with our current behavioral goals. Both bottom-up and top-down selection can be spatial or feature-based. Spatial selection involves the selection of a stimulus at a specific location, for example an object presented at the left side of a display. Feature-based selection involves the selection of a stimulus with a specific feature. A typical example of feature-based selection is the selection of a specific color from other colors that are present in the visual field. The present thesis is concerned with bottom-up and top-down feature-based selective attention. The first chapter introduces the relevant terms and provides the background to the empirical Chapters 2 - 5.

Chapter 2 contains a study of the time course of color- and luminance-based salience effects. In two experiments, we investigated how salience derived from color and luminance differences influences covert visual attention over time. We presented observers with a display consisting of two distinct color (Experiment 1) or luminance singletons (Experiment 2) embedded in a field of homogeneously oriented lines which was masked after six different stimulus-onset-asynchronies. Observers had the task to indicate the location of a probe within the mask. A comparison of reaction times to the probe at the location of the more salient singleton, the less salient singleton and a background location revealed that the relative salience of the singletons affected covert attention only briefly.
after stimulus onset. The mere presence of a singleton object, however, affected selection for a much longer time span.

Chapter 3 comprises a study of feature-based selection in neglect and extinction patients. In two experiments, we asked a group of patients with extinction and with and without additional neglect to make a direct saccade to one of two differently oriented lines within a field of homogenous background lines. We varied the relative salience of these lines by changing the orientation of the background elements. We measured the endpoint and the saccadic latency of the first saccade after display onset to determine speed-accuracy functions for each condition and participant. Using a multinomial model, we decomposed these functions into the underlying top-down or goal-driven and bottom-up or stimulus-driven components. This analysis revealed that stimulus-driven processing of stimuli in the more severely affected hemi-field was initially present, but reduced in comparison to the less affected hemi-field and in comparison to a control group. Goal-driven processing was overall reduced in the patients. Experiment 2 showed that this pattern of results did not depend on an overall spatial bias toward the less affected hemi-field.

Chapter 4 describes a study of the time course of working memory effects on visual attention. In five experiments, we asked participants to memorize a color, which was either difficult or easy to verbalize. They then searched for an unrelated target in a visual search display and finally completed a memory test. In half of all trials, one of the distractors in the search display had the memorized color. In the other half of all trials, the color of all distractors differed from the memorized color. We varied the time between the to-be-remembered color and the search display, as well as the ease with which the colors could be verbalized. We found that when the to-be-remembered color reappeared in the search display and was difficult to verbalize, response times to the target were longer than when the memorized color did not reappear. This suggests that the memory item attracted the participants’ attention and thus delayed the response to the target. However, when the to-be-remembered color was easy to verbalize, the influence of the working memory item on visual search decreased with increasing time between the presentation of the memory item and the search display. Working memory effects on visual search also decreased when the duration of visual encoding was limited by an additional task or when the memory item was presented only briefly. We concluded that for working memory effects on visual attention to be sustained, a sufficiently strong visual representation is necessary.

Chapter 5 contains a study of the costs of attentional set switching. In two experiments, we asked observers to sequentially saccade towards two color-defined targets, one on the left side of the display and the other on the right, each among heterogeneously colored distractors. The targets were either of the same color (no switch condition) or of different colors (attentional set switch condition). Each color was consistently tied to one side, allowing observers to maximally prepare for the switch. We found that saccades were both slower and less accurate in the switch condition than in the no switch condition. Further, whenever one of the distractors had the color associated with the other attentional set, a large proportion of saccades did not end on the target, but on this distractor.
A time course analysis revealed that the preference for the distractor associated with the old set turned into a preference for the target (associated with the new set) after about 250 to 300 ms, which suggests that this is the time required to switch attentional sets.
Het tijdsverloop van stimulusgedreven en doelgerichte visuele selectie
De visuele omgeving bevat een enorme hoeveelheid informatie, waarvan het meeste niet relevant is voor onze doelstellingen. Desalniettemin is het wel van belang dat wij in staat zijn om dat deel van die informatie te selecteren dat nodig is om doelmatig te handelen. Dit betekent dat de hersenen de moeilijke taak hebben om relevante informatie te selecteren en irrelevante informatie te negeren. Deze taak wordt volbracht met behulp van een mechanisme met de naam selectieve aandacht. Selectieve aandacht geeft prioriteit aan een aantal stimuli in het gezichtsveld over anderen, zodat ze worden verwerkt met meer capaciteit. Er wordt aangenomen dat selectieve aandacht wordt aangestuurd door twee mechanismen: een stimulusgedreven mechanisme en een doelgericht mechanisme. Het stimulusgedreven mechanisme geeft prioriteit aan stimuli die opvallend zijn in vergelijking met hun lokale omgeving. Deze stimuli kunnen bijvoorbeeld een unieke kleur of orientatie hebben, zich tussen statische omringende elementen bewegen of verschillen in grootte ten opzichte van de andere stimuli. Het doelgerichte mechanisme geeft prioriteit aan die stimuli die in overeenstemming zijn met onze doelstellingen. Stimulusgedreven en doelgerichte selectie kunnen zowel op basis van plaats als op basis van een stimuluskenmerk plaatsvinden. Met plaatsbepaalde selectie wordt de selectie van een stimulus op een bepaalde locatie bedoeld, bijvoorbeeld wanneer een object aan de linker kant van een beeldscherm wordt geselecteerd. Met kenmerkgebaseerde selectie wordt de selectie van een stimulus met een bepaald kenmerk bedoeld. Een typisch voorbeeld van kenmerkgebaseerde selectie is de selectie van een specifieke kleur tussen andere kleuren. Dit proefschrift onderzoekt de rol van stimulusgedreven en doelgerichte selectieve aandacht op basis van stimuluskenmerken. Het eerste hoofdstuk introduceert de relevante begrippen en voorziet in een theoretische achtergrond ten behoeve van de empirisch georiënteerde hoofdstukken 2-5.

Hoofdstuk 2 bevat een studie naar het tijdsverloop van kleur en luminantie gebaseerde opvallendheidseffecten. We hebben onderzocht in hoeverre de opvallendheid bepaald door kleur- en luminantieverschillen de visuele aandacht over de tijd beïnvloedt. Proefpersonen kregen een beeldscherm te zien met daarop twee verschillende door kleur- (Experiment 1) of luminantieverschillen bepaalde unieke elementen (Experiment 2) ingebed in een veld van homogege georienteerde achtergrondlijnen. Het beeldscherm werd na zes verschillende tijdsintervallen gemaskerd. Proefpersonen hadden de taak om de locatie van een imperatief signaal in de maskering aan te geven. Een vergelijking van de reactietijden op het signaal op de locatie van het meer opvallende unieke element, het minder opvallende element en een achtergrondlijn, liet zien dat de effecten van de relatieve opvallendheid van een element op aandacht kortdurend zijn. De aanwezigheid van een uniek element beïnvloedde het selectiedrag gedurende een langere periode.

Hoofdstuk 3 omvat een studie naar de op kenmerken gebaseerde selectie van neglect en extinction patienten. In twee experimenten, vroegen we een groep neglect en extinction patienten om een oogbeweging te maken naar een van twee uniek georiënteerde lijnen ingebed in een veld van homogege georien-
teerde achtergrondlijnen. We varieerden de relatieve opvallendheid van deze lijnen door de orientatie van de achtergrondlijnen te veranderen. We maten het eindpunt en de saccade latentie van de eerste oogbeweging apart voor iedere conditie en deelnemer om op die wijze snelheidsnauwkeurigheid functies te kunnen bepalen. Met behulp van een multinomiaal model konden we de functies ontdelen in de onderliggende doelgerichte en stimulusgedreven componenten. Uit deze analyse bleek dat de stimulusgedreven verwerking van stimuli in het aangedane hemiveld gereduceerd was in vergelijking met de verwerking in het minder aangedane hemiveld en in vergelijking met de controle groep. Uit de resultaten van Experiment 2 bleek dat dit patroon van resultaten niet afhankelijk was van de aanwezigheid van een algemeen ruimtelijke afwijking naar het minder aangedane hemiveld.

Hoofdstuk 4 beschrijft een studie naar het tijdsverloop van werkgeheugen effecten op visuele aandacht. In vijf experimenten vroegen we de deelnemers om een kleur, die moeilijk of gemakkelijk te verwoorden was, te onthouden. Volgens hadden zij de taak om te zoeken naar een aan de kleur ongerelateerd doelobject, gevolgd door het voltooien van de geheugentak. In de helft van de trials was de kleur van een van de irrelevante afleiders gelijk aan de te onthouden kleur. In de andere helft van de trials werd de kleur van alle irrelevante afleiders af van de te onthouden kleur. We varieerden de tijd tussen de aanbieding van de te onthouden kleur en de aanbieding van het zoekbeeldscherm en we varieerden het gemak waarmee de te onthouden kleur te verwoorden was. We vonden dat wanneer de te onthouden kleur aangeboden werd in het zoekbeeldscherm en moeilijk te verwoorden was, de reactietijd langer was dan wanneer de te onthouden kleur niet werd aangeboden. Dit suggereert dat de te onthouden kleur de aandacht trok en daarmee de vertraagde reactietijd op het doel bewerkstelligde. Echter, wanneer de te onthouden kleur gemakkelijk te verwoorden was, werd de invloed van de aanwezigheid van zo’n kleur in het geheugen minder met toenemende tijd tussen de aanbieding van de te onthouden kleur en het zoekbeeldscherm. Werkgeheugen effecten op visueel zoeken namen ook af wanneer de duur van de visuele encodering werd beperkt door een extra taak of door een korte presentatie van het geheugenitem. We concludeerden dat er een sterke visuele representatie nodig is voor het verkrijgen van aanhoudende geheugen effecten op visuele aandacht.

Hoofdstuk 5 bevat een studie naar de kosten van het schakelen tussen twee verschillende aandachtssets. In twee experimenten, hebben we aan proefpersonen gevraagd om achtereenvolgens een oogbeweging te maken naar twee uniek gekleurde doelobjecten waarvan een aan de linker kant en een aan de rechterkant van het beeldscherm werd aangeboden. Aan beide kanten van het beeldscherm werden de doelobjecten aangeboden tussen heterogeen gekleurde afleiders. De doelobjecten hadden ofwel dezelfde kleur (geen schakeling conditie) of verschillende kleuren (schakeling conditie). Iedere doelobject kleur was consistent verbonden met een kant van het beeldscherm waardoor de proefpersonen zich maximaal konden voorbereiden op een setschakeling. We vonden dat de oogbewegingen langzamer werden geinitieerd en minder nauwkeurig waren in de schakeling conditie relatief ten opzichte van de geen schakeling.
conditie. Verder bleek dat wanneer de kleur van een van de afleiders gelijk was aan die van de target in de andere aandachtsset, er veel oogbewegingen gericht waren naar deze afleider in plaats van naar het doelobject. Een analyse van het tijdsverloop van de effecten liet zien dat deze voorkeur voor een irrelevante afleider veranderde in een voorkeur voor het doelobject (geassocieerd met de nieuwe aandachtsset) na ongeveer 250 tot 300 ms. Dit suggereert dat dit de tijd is die nodig is om te schakelen tussen aandachtssets.
Bibliography


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