Neural mechanisms of global attention- and reward-related selection in human visual cortex

Thesis

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Table of contents

List of abbreviations and acronyms……..….5

Summary ……..….6

Zusammenfassung……..…..7

I. - General Introduction……..8

1.1 Visual Attention..……....8

1.2 Spatial Attention..……..…....9

1.3 Feature-Based Attention..……..….11

1.3.1 Feature-Based effects in the spatial focus of attention..……..….12

1.3.2 Global feature selection of attention……...12

1.4 Object-Based Selection of Attention.…..…….15

1.5 Computational approach for attentional feature selectivity: Selective Tuning Model…..…17

1.6 Reward-based biasing of visual selectivity..……..…...17

1.7 Influence of past selection history on ongoing visual selection……..……..……19

II. Motivation……..22

III. General Methods…….….25

3.1 Subjects…….…….25

3.2 Experimental design…….25

3.3 Stimuli ……....26

3.4 Data acquisition ……...26

3.5 Preprocessing of electrophysiological data……...….28

3.6 Alignment of individual head positions (repositioning MEG data)…….....29

3.7 Statistical analysis of data…..…….....30

3.8 Current sources estimates ……..…....31

IV. Empirical Work……..…..…32

Part 1 Neuromagnetic indices of global feature selection in the human visual cortex

4.1 Experiment 1…….…….....32

4.1.1 Subjects…….....…32

4.1.2 Stimuli…….……32

4.1.3 Task……..34

4.1.4 Data recording and statistical analysis..……..…34

4.1.5 Neurophysiological results..……..35

4.1.5a Adaptation…….....37

4.1.5b Distractor Suppression…….38

4.1.5c Attentional Tuning……..….38

4.1.6 Conclusions …….....39

4.2 Experiment 2…….....40

4.2. Experiment 2 Section A…….....41

4.2.A-1 Subjects……....41

4.2.A-2 Stimuli…….....41

4.2.A-3 Task and procedure……..…...41

4.2.A.4 Results…….....41

4.2.A.5 Conclusions…….....43

4.2. Experiment 2 Section B…….....43

4.2.B.1 Subjects…….....45

4.2.B-2 Stimuli…….....46

4.2.B-3 Task..…….....47

4.2.B.4 Data analysis……..…….....47

4.2.B.5 Behavioral Results……..…..…47

4.2.B.6 Neurophysiological data……..……...48

4.2.B.7 Conclusions……..…….....49

Part 2: Neuromagnetic indices of global attention- and reward-related selection in the human visual cortex

4.3 Experiment 3 ……52

4.3. Experiment 3 Section A……53

4.3.A-1 Subjects……53

4.3.A-2 Stimuli……53

4.3.A-3 Task and procedure……53

4.3.A.4 Behavioral results……54

4.3.A.5 Conclusions……54

4.3. Experiment 3 Section B……54

4.3.B.1 Subjects ……54

4.3.B.2 Stimuli……55

4.3.B.3 Task and procedure……56

4.3.B.4 Reward-schedule……56

4.3.B.5 Data recording and analysis……56

4.3.B.6 Behavioral Results……57

4.3.B.7 Neurophysiological data……59

4.3.B.8 Conclusions……60

4.4 Experiment 4……61

4.4.1 Subjects……61

4.4.2 Stimuli ……61

4.4.2.1 Attended stimuli ……62

4.4.2.2 Probe stimuli and probe conditions……62

4.4.3 Task……63

4.4.4 Reward schedule……64

4.4.5 Data recording and analysis……64

4.4.6 Behavioral Results……64

4.4.7 Neurophysiological data……65

4.4.7.1 Response to target probes……65

4.4.7.2 Response to reward color probes……..67

4.4.8 Conclusions……..69

V. General Discussion……..70

5.1 Experiment 1……..70

5.1.1 The Temporal dynamics of GCBA is not altered by continuous attention to the attended color……..70

5.1.2 Attenuation of the N1 response……..71

5.1.2a Low-level sensory adaptation as an account of the N1 attenuation.....71

5.1.2b The N1 attenuation reflects distractor suppression……..72

5.1.2c Selective tuning as an account of the N1 attenuation.....72

5.2 Experiment 2……..72

5.2.1 Tuning of the target template representation is reflected by attenuation of the N1 response……..72

5.2.2 Attenuation of the N1 does not reflect distractor suppression……..73

5.2.3. Color target selection based on the off-target gain as an alternative to on-target selective tuning……..73

5.2.4 Enhanced amplitude of the N2 response reflects color selection under conditions of high-task demands……..73

5.3 Experiment 3……..74

5.3.1 GCBA and GRBS dissociate at the top-down level……..74

5.3.1.1 The T-response is already at ceiling on hard trials……..74

5.3.1.2 TR color combination was coded as the "true reward" instead of R-color alone……..75

5.4 Experiment 4……..75

5.4.1 Response to target probes……..75

5.4.2 Response to reward probes……..76

5.4.3 Coding of reward-related colors bias in visual cortices……..77

6. Perspectives and Future Research…….....78

6.1 Selective tuning or gain enhancement of the off-target signals……..……78

6.2 Task-load as an account of the attenuation of the N1……...…….79

7. References. …….....81

List of abbreviations and acronyms

ACC: Accuracy
BOLD: Blood Oxygenation Level
CSD Current Source Estimates
EEG: Electroencephalography
EOG: Electrooculogram
ERP: Event-Related Potential
ERMF: Event-Related Magnetic Field
ERPSS: Event-Related Potential Software System
fMRI: functional Magnetic Resonance Imaging
GCBA: Global Color Based-Attention
GFBA: Global Feature Based-Attention
GRBS: Global Reward Based-Selection
HEOG: Horizontal electrooculogram
ISI: Inter-stimuli Interval
LVF: Left Visual Field
MEG: Magnetoencephalography
MNI: Montreal Neurological Institute brain template.
MNLS: Minimum Norm Least Squares
MT: Middle Temporal area
pT: picoTesla
RANOVA: Repeated measures Analysis of Variance
RT: Response Time
RVF: Right Visual Field
SN: Selection Negativity
SSVEP: Steady-State-Visual Evoked Potentials
SA: Surround Attenuation
ST: Selective Tuning model
uv: microvolt
V1: Primary Visual area
V4: Visual area V4
VEOG: Vertical electrooculogram

Summary

Selective attention to color, motion, orientation, size, or spatial frequency enhances the neural response in visual cortical areas responsible for processing these features. Such neural bias occurs in a spatially global manner such that task-relevant features are also selected in unattended locations. This phenomenon is called global feature-based attention (GFBA). Analogously, features associated with reward elicit an enhanced brain response irrespective of whether they are presented in attended or in unattended locations (GRBS: global reward-based selection). Although several studies have characterized neural correlates of GFBA, many questions remain open. The first part of the current work sheds some light on the cortical mechanism underlying GFBA and its temporal dynamics (Experiment one and two). The second part focuses on the relationship between GFBA and GRBS (Experiment three and four).

To assess neural correlates of GFBA and GRBS, the electrical and magnetic brain responses were recorded using both EEG and MEG at the same time subjects performed different versions of the unattended probe paradigm. In this paradigm, two stimuli are presented simultaneously in opposite visual fields, with one being attended to perform the task (attended stimulus), and the other one being unattended (task-irrelevant probe). GFBA and GRBS responses are then reflected by the neural response elicited by the unattended probes as a function of whether they do or do not match the relevant target color (GFBA) or the reward-associated color (GRBS).

Experiment one investigates whether the color selection process (GFBA) occurs already during the early processing of information (first feedforward sweep) or emerges at later stages of processing (feedback activity). Experiment two was designed to clarify as to whether color selectivity is caused solely by the enhancement of the attended color, or whether it also entails the attenuation of surrounding (i.e., similar) color-values. Data from experiment one confirmed that GFBA modulations appear only late (>160ms) in the time range of feedback signals, even when color information was continually driving the feedforward sweep of information by the presentation of a continuous color stream. Importantly, when the task required fine color discrimination, an attenuation of the GFBA response could be observed in the time range of the N1 component (~200ms). This attenuation was found both in experiment one when continuous presentations of closely similar colors preceded the target color and in experiment two when the target was presented next to a very similar distractor color.

Experiment three tests, whether GFBA and GRBS responses can be successfully dissociated to some extent. To this end, the attentional load was manipulated, while reward assignments were kept constant. Increasing attention demands did increase the response to the attended, task-relevant color, while the response to the reward color remained mostly unchanged. This differential increment in the response amplitude indicates that GFBA and GRBS responses in visual cortical areas operate independently, and both responses are, indeed, dissociable. Experiment four extends those findings by showing that global feature and reward biases can also be found for colors that are currently irrelevant but have been a target or reward-associated color in previous experimental blocks (attention and reward priming). Those priming effects emerge early in the visual cortex (around ~70-120ms), indexing a feature relevance bias at the perceptual level.

Taken together, the current experiments reveal spatially global selection biases for both attended and rewarded colors. Although attention and reward influence the same feature-selective areas in the extrastriate visual cortex, the underlying neural modulations seem to be largely independent.

Zusammenfassung

Das Richten der Aufmerksamkeit auf Farbe, Bewegung, Orientierung, Größe oder räumliche Frequenz, verstärkt die neuronale Antwort in den für die Verarbeitung dieser Merkmale zuständigen visuellen kortikalen Arealen. Dieser neurale „Bias" tritt räumlich global auf, so dass die aufgabenrelevanten Merkmale auch an unbeachteten Orten ausgewählt werden. Dieses Phänomen wird als globale merkmalsbasierte Aufmerksamkeit („Global Feature-Based Attention", GFBA) bezeichnet. Analog hierzu rufen mit Belohnung assoziierte Merkmale ebenfalls eine verstärkte Hirnantwort hervor, unabhängig davon, ob sie an beachteten oder unbeachteten Orten präsentiert werden („Global Reward-Based Selection", GRBS). Obwohl etliche Studien die neuronalen Korrelate von GFBA charakterisiert haben, bleiben noch viele Fragen offen. Der erste Teil der vorliegenden Arbeit trägt zur Klärung des der GFBA zugrundeliegenden kortikalen Mechanismus sowie dessen zeitlicher Dynamik bei (Experiment eins und zwei). Der zweite Teil fokussiert auf die Beziehung zwischen GFBA und GRBS (Experiment drei und vier).

Um die neuronalen Korrelate von GFBA und GRBS zu erfassen, wurden die elektrischen und magnetischen Gehirnantworten mittels EEG und MEG aufgezeichnet, während die Probanden verschiedene Versionen des „unattended probe paradigm" durchführten. In diesem Paradigma werden zwei Stimuli gleichzeitig in entgegengesetzten visuellen Feldern dargestellt, wobei einer von ihnen zur Ausführung der Aufgabe benötigt und somit beachtet wird („attended stimulus"), während der andere irrelevant ist und unbeachtet bleibt („task-irrelevant probe"). Die GFBA- und GRBS-Antworten werden durch die neuronale Antwort zur unbeachteten Probe reflektiert. Man vergleicht hierbei Gehirnantworten zu Probes in der relevanten Zielfarbe (GFBA) oder in der aktuellen Belohnungsfarbe (GRBS) mit Antworten zu Probes in anderen, irrelevanten Farben.

In Experiment 1 wurde untersucht, ob der Farbselektionsprozess bei der GFBA bereits während der frühen Phase der Informationsverarbeitung (im „first feedforward sweep") auftritt oder sich erst in späteren Verarbeitungsphasen (als „feedback activity") zeigt. Experiment zwei sollte zudem klären, ob die Farbselektivität ausschließlich durch die Verstärkung des Signals der beachteten Farbe entsteht oder ob sie auch eine Abschwächung umgebender (d.h. ähnlicher) Farben mit sich bringt. Daten aus Experiment 1 bestätigten, dass GFBA-Modulationen ausschließlich spät, im Zeitbereich von Feedbacksignalen, zu finden sind (>160 ms nach Stimulus-Onset), selbst wenn der Feedforward Informationsfluss durch eine kontinuierliche Farbpräsentation (einen „Farbstrom") angetrieben wird. Wenn die Aufgabe eine feine Farbunterscheidung erforderte, konnte interessanterweise eine Attenuierung der GFBA-Antwort im Zeitbereich der N1-Komponente (~200ms) beobachtet werden. Dies wurde sowohl in Experiment 1 festgestellt, wenn der Zielfarbe kontinuierliche Präsentationen von sehr ähnlichen Farben vorausgingen (zeitliche Nähe von ähnlichen Farben) als auch in Experiment 2, wenn der Zielstimulus (das „target") räumlich neben einer sehr ähnlichen Distraktorfarbe präsentiert wurde (räumliche Nähe von ähnlichen Farben).

In Experiment drei wurde getestet, ob GFBA- und GRBS-Antworten erfolgreich dissoziiert werden können. Zu diesem Zweck wurde die Aufmerksamkeitslast („attentional load") manipuliert, während die Belohnungszuweisungen unverändert blieben. In der Tat erhöhten zunehmende Aufmerksamkeitsanforderungen tatsächlich die Gehirnantwort zur beachteten, aufgabenrelevanten Farbe, ließen aber die Gehirnantwort zur Belohnungsfarbe größtenteils unverändert. Auf diese Weise konnte gezeigt werden, dass GFBA- und GRBS- Gehirnantworten unabhängig voneinander manipuliert werden können und tatsächlich zu einem gewissen Grad dissoziierbar sind. Experiment 4 ergänzt diese Ergebnisse, indem es Effekte globaler Merkmals- und Belohnungsselektion sogar für aufgabenirrelevante Farben zeigt, solange diese in vorhergehenden experimentellen Blöcken als Ziel- oder Belohnungsfarbe verwendet wurden (sogenannte „Priming Effekte" der Aufmerksamkeits- und Belohnungsselektion). Diese Priming-Effekte, die früh im visuellen Kortex zu finden sind (ca. 70-120ms nach Stimulus-Onset), zeigen einen Merkmalsrelevanz-Bias, der bereits auf Wahrnehmungsebene stattfindet.

Zusammengenommen zeigen die Experimente räumlich globale Selektionsprozesse sowohl für beachtete als auch für belohnte Farben. Obwohl Aufmerksamkeit und Belohnung die gleichen merkmalselektiven Bereiche im extrastriären visuellen Kortex beeinflussen, scheinen die zugrunde liegenden neuronalen Modulationen weitgehend unabhängig voneinander zu sein.

I. General Introduction

The present work focuses on cortical mechanisms underlying global feature selectivity elicited by task-related (attention, GFBA) and reward-related associations (GRBS).

The first part investigates the temporal dynamics of neural mechanisms underlying global feature-based attention (GFBA; task-related). Specifically, it asks at what stage of visual processing GFBA operates. Does GFBA to color (global color-based attention, GCBA) influence the initial feedforward sweep of information processing or does it exclusively operate at later feedback stages of signal processing. Furthermore, we address the role of discrimination demands on GCBA. We ask to what extent fine discrimination of color would involve the attenuation of nearby color-values in color space as predicted by influential computational accounts of visual attention like the selective tuning model (STM, Tsotsos, 2011). The second part of this work investigates the relationship between the GCBA and the global color response elicited by colors associated to reward. Attention and rewards are associated with very similar global activity modulations in the visual cortex. Here, we asked whether they could nonetheless be dissociated at some level of cortical representation. Additionally, we test the role of implicit color priming effects on GCBA and reward-based selectivity biases. We particularly ask whether implicit biases would dissociate between attention and reward.

The following paragraphs offer a brief theoretical framework to set the stage for the research questions, and hypotheses put forward here. First, relevant frameworks of attentional selection, such as space-based selection, feature-based selection, and object-based selection, are briefly described. Then, a brief review of reward-based selection and past selection history on ongoing visual selection is described.

1.1 Visual Attention

In visual processing, attention is defined as a collection of brain mechanisms that allow focusing on relevant information while ignoring the irrelevant one. Importantly, visual attention is not a unitary process, but instead relies on several selection mechanisms simultaneously operating flexibly and dynamically on different visual representations.

From a cognitive standpoint, attention is defined as a selective process dealing with the overload of information that observers experience at any given moment. Attention is the process that deals with this limit by filtering unwanted information.

From the computational modeling perspective, visual attention is a mechanism that solves complexity issues of visual representation (Tsotsos, 2005). Visual processing is formulated as a combinatorial problem of evaluating all possible item representations. In conditions of no-selectivity, parallel processing of all items would lead to an exponentially increasing number of possible input representations, which makes the problem of visual selection intractable (Koch & Ullman, 1985; Tsotsos, 1990, 2011). Attention is considered the mechanism that reduces the number

of information by tuning the visual processing network to make the visual selection process a spatiotemporally tractable operation.

Whether attentional effects occur at early or late processing stages during the processing of information has been debated in the literature (Deutsch & Deutsch, 1963; Lachter, Forster, & Ruthruff, 2004; Norman, 1968; Treisman, 1969). On the one hand, the early selection hypothesis proposed that relevant stimuli are selected based on their basic features such as color, orientation, or pitch before stimulus identification. Therefore, early selection is a bottleneck defining the capacity limit to avoids overload by irrelevant information (Broadbent, 1958 cited in Lachter, Forster, & Ruthruff, 2004; Treisman, 1969). In contrast, late selection theorists have argued that relevant and irrelevant stimuli are thoroughly analyzed, and only after perception, stimuli are selected to be stored or not in memory (Deutsch & Deutsch, 1963; Norman, 1968). Beyond those historical concepts, visual attention turns out to be not a unitary process; it instead consists of a set of mechanisms that depend on the type and quality of information and the task demands.

1.2 Spatial Attention

Directing our attention to locations can be performed either by moving the head and eyes to selected regions (overt-attention) or by purely changing our attentional focus to spatial locations in the scene while keeping the retinal image constant (covert-attention) (Posner, 1980). Hermann von Helmholtz was the first describing the effects of cover attention early in 1866 (Helmholtz & Southall, 1924). He emphasized our ability to direct attention by merely using a conscious and voluntary effort without moving eyes (Yantis, 1998).

Later, Posner and coworkers documented more systematically how attention can be shifted to locations independent of eye movements by using the cueing paradigm. The cueing paradigm consisted of presenting a spatial cue before stimulus onset indicating the location of the upcoming target. In this task, three types of trials were tested: i) when cue indicated the location of the target (valid trials), ii) when cue indicated the opposite location of the target (invalid trials) iii) when no-cue was presented (neutral trials). The response to targets preceded by valid cues was significantly facilitated (faster Response Time =RTs) relative to trials with neutral or invalid cues (Posner, 1980).

Amplitude variations indexed the benefits and costs of cueing in the electrophysiological response, particularly in the P1 and N1 components of Event-Related Potentials (ERPs). Component responses appearing between 90-130ms and 150-200ms were larger for validly cued targets relative to non-cued or invalid cued target locations (Harter, Anllo-Vento, & Wood, 2018; Mangun & Hillyard, 1991). Although these studies showed that spatial attention modulated both P1 and N1 components, later studies showed that the two components reflect two different processes. The P1-amplitude modulation is more related to spatial selection (Luck et al., 1994; Luck & Hillyard, 1995), and the N1 amplitude modulation is more related to discrimination processes within the selected location (Luck et al., 1994; Mangun & Hillyard, 1991). Similarly, there is an agreement within the literature that the increment of amplitude in the P1 and N1 components by spatial selection reflects the amplification of neural activity or a gain enhancement of sensory processing in the visual cortical areas (Hillyard, Vogel, & Luck, 1998; Salinas & Sejnowski, 2001; Salinas, Thier, & Jolla, 2000).

Spatial attention effects have been observed in the early visual cortices and extrastriate visual areas (contralateral to attended targets) by using neuroimaging techniques (Kastner, Pinsk, Weerd, Desimone, & Ungerleider, 1999). Spatial attention effects influencing the early stages of visual processing in the Lateral Geniculate Nucleus have also been validated using fMRI (O'Connor, Fukui, Pinsk, & Kastner, 2002), and neurophysiological recordings in monkeys (McAlonan, Cavanaugh, & Wurtz, 2008). These documented modulations in the initial subcortical stages suggested that spatial attention influences the first feedforward processing in the visual system (McAlonan et al., 2008).

Attentional deployment can be guided not only by location cueing but also without it. For example, in visual search tasks, target identification can be guided by features such as color, orientation, shape, spatial frequency, oddity, etc. The timing of location selection depends on the uniqueness of target definition, the number of distractors in the display, and the similarity between target and distractors (Treisman, 1991; Wolfe, 1994). Neurophysiological studies using visual search tasks revealed that the target elicited a larger N2 response at posterior and contralateral sites to the target. This amplitude modulation was called N2pc (Luck & Hillyard, 1994). The N2pc component is a negative wave elicited at the contralateral side to the target, and it is larger for targets accompanied by distractors that share features with the target. The N2pc component is assumed to reflect a spatial filtering process (Luck & Hillyard, 1994b). Hickey and coworkers (Hickey, Di Lollo, & McDonald, 2009) additionally suggested that the N2pc component indexes two operations. The negativity elicited by targets (N_T) over electrode sites contralateral to the target. And a distractor (P_D) positivity, typically contralateral to a distractor (ipsilateral to the target). Hopf and colleagues (Hopf et al., 2000) reported that the N2pc component (using MEG recordings) is composed of two main cortical sources, one in parietal regions (180-220ms) and the other in the posterior-inferotemporal and anterior occipital regions (220-240ms). Interestingly the later regions are associated with mechanisms for resolving ambiguity between target and distractors during visual search tasks (Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002) consistent with ambiguity resolution account of the N2pc (Luck et al., 1997).

Another relevant question is the distribution or the profile of the spatial focus of attention. While several mechanisms leading to different distribution profiles have been discussed over the years, they fall into three main conceptualizations: a spotlight, a pair of zoom lenses, and a gradient profile. Posner described the focus of attention as a spotlight, the information contained or covered by the beam is better detected and discriminated in comparison with information located outside of the spot (Posner, 1980; Posner, Snyder, & Davidson, 1980). Eriksen and Yeh (Eriksen & Yeh, 1985; Schad & Engbert, 2012) suggested an extension that attentional resources could be better described as zoom lenses so that depending on the coverage within the visual field, the resolution varies. Thus, when attentional resources are distributed over the whole visual field, the resolution is low. In contrast, when attentional resources are restricted to small regions, the resolution and power of processing are high. Finally, recent experimental data have suggested that the profile of the focus of attention might dynamically vary between a Gaussian gradient and a Mexican hat-shape. Based on behavioral indices, for example, it has been shown that benefits of enhanced sensory processing fall off gradually when varying the eccentricities from infrequent targets relative to central cued target-location (Shulman, Wilson, & Sheehy, 1985). Similarly, behavioral and neurophysiological responses (MEG recordings) to probes have shown a center-surround profile

(Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2009; Hopf et al., 2006; Hopf, Boehler, Schoenfeld, Heinze, & Tsotsos, 2010; Tsotsos et al., 1995).

1.3 Feature-based attention

Attending selectively to features such as color, motion, orientation, size, and spatial frequency enhances the neural response in visual cortical areas specialized for processing those features. This mechanism is known as feature-based selection of attention (FBA) (Mcadams & Maunsell, 2000; Motter, 1994b, 1994a). Behavioral studies using visual search tasks showed that FBA improves detection and enhances the performance of color-defined (Bauer, Jolicoeur, & Cowan, 1996; D'Zmura, 1991; Nagy & Sanchez, 1990; Treisman & Gormican, 1988), motion-defined (McLeod, Driver, & Crisp, 1988; Müller & Von Mühlenen, 1999; Rosenholtz, 2001), orientation-defined targets (Foster & Ward, 1991; Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992; Wolfe, Klempen, & Shulman, 1999). Analogous beneficial effects were found for features like size and spatial frequency (Sagi, 1988; Treisman & Gormican, 1988).

Several neurophysiological studies have reported an increment of the neural response (single-unit recordings) of these neurons more selective to the attended feature-values. (Bichot, Rossi, & Desimone, 2005; Bichot & Schall, 1999; Buracas & Albright, 2009; Mcadams & Maunsell, 2000; Motter, 1994a, 1994b). For example, Motter and coworkers (Motter, 1994a, 1994b) showed that the firing of neurons in V4 (extrastriate visual area) roughly doubled around 200ms after stimuli onset when the current feature (color or luminance) matched the previously cued feature but not when it did not match. Similar effects were observed in area MT of monkeys (selective for motion processing), while monkeys performed a covert search task for targets defined by color and motion direction (Buracas & Albright, 2009). Neural responses in MT were modulated when the selected stimuli matched the previous cued combination of color and motion direction (~400ms before) relative to non-targets trials, which were different in color and motion direction.

A study conducted by Bichot and coworkers (Bichot et al., 2005) showed that response of neurons (V4) with RFs selective to cued features (color, shape or color and shape) was enhanced and synchronized (gamma band) relative to the response to non-cued features or from non-selective neurons. Larger increment of the response was observed when both cued and preferred conditions were together. Notably, such enhancement effect for features occurred throughout the visual field so that responses to distractors located apart from target but sharing the same color with the cue were also enhanced (global feature-based attention, cf. 1.3.2).

Although the previously described behavioral and neurophysiological findings in visual search tasks broadly support FBA effects, some precisions are required. The observed response consisted of a combined effect of spatial (covert and overt)- and feature-based influences. The experimental designs used in those experiments determine that simultaneously the target feature guides selection a spatial component guides when finding the target throughout the visual field.

In the following paragraphs, I will describe the main findings of studies focused on feature-based selection effects dissociated from the spatial selection effects.

1.3.1 Feature-based effects in the spatial focus of attention

Dissociating FBA effects from spatial contributions is achieved by doing two things: fixing the spatial location of the attended stimulus, and varying the number of features/feature values of the attended stimulus (switching attention to one or other features without changing the attended location). Typical examples are overlapping dots moving in different directions or overlapping gratings with different orientations. Manipulating these two parameters allowed comparing the response between features when they are attended versus unattended at the same location.

Andersen and coauthors (Andersen et al., 2008) used steady-state visual evoked potentials (SSVEP) to show that selective attention to color enhances the neural response relative to unattended colors when both are located in the same attended region. Andersen's et al., study (Andersen et al., 2008) used spatially intermingled red-blue dots displayed in the center, moving randomly and flickering at different frequencies. Frequency tagging allowed analyzing the SSVEP elicited by each color. The SSVEP in the early visual cortices was modulated depending on whether the color was attended or not (Andersen, Hillyard & Müller, 2008; Müller et al., 2006). When color and orientation were combined, and both features were simultaneously attended (feature-conjunction targets), the SSVEP amplitude was the sum of both single amplitudes when attended separately (Andersen, Müller & Hillyard, 2015).

Furthermore, Schoenfeld and coworkers (Schoenfeld et al., 2007), using combined EEG-MEG and fMRI recordings, documented that enhanced response to attended features occurred mainly in cortical areas specialized in processing attended features (color or motion). In this study, subjects were instructed to detect as soon as possible either color change (white to red/orange) or speed of movement of 100 stationary dots centrally located. At the beginning of each block, independent cues for color and motion detection were displayed. In both cases, the response began after ~120ms-350ms (attended vs. unattended), and the neuroimaging data confirmed that when color was attended, the response increased bilaterally in V4 areas. In contrast, when the motion was attended, the response increased bilaterally in V5/human-MT+ regions.

Other neuroimaging studies using fMRI recordings have also confirmed modulations of neural activity in areas specialized for attended features like motion (Beauchamp, Cox, & DeYoe, 1997; Chawla, Rees, & Friston, 1999; Liu, Slotnick, Serences, & Yantis, 2003; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Shulman et al., 1999; Watanabe et al., 1998) and color (Chawla, Phillips, Buechel, Edwards, & Friston, 1998; Schoenfeld et al., 2007).

1.3.2. Global feature selection of attention

As described earlier, the feature-based selection of attention operates by increasing the neural response to attended features to the degree to which the input matches the tuning of cells in feature selective regions. FBA effects seem to operate in parallel throughout the visual field without being confined to the spatial attended area. The global nature of FBA, also known as global feature-based attention (GFBA) has been described and supported by numerous

neurophysiological studies in monkeys and humans and also by neuroimaging work (Andersen, Hillyard, & Muller, 2013; Bartsch, Donohue, Strumpf, Schoenfeld, & Hopf, 2018; Bartsch et al., 2017; Bichot et al., 2005; Bondarenko et al., 2012; Moher, Lakshmanan, Egeth, & Ewen, 2014; Saenz, Buracas, & Boynton, 2002; Sàenz, Buraĉas, & Boynton, 2003; Stoppel et al., 2012; Treue & Martinez-Trujillo, 1999; Zhang & Luck, 2009)

Bichot and coworkers (Bichot et al., 2005)., for example, reported that the response of neurons in the V4 brain area of monkeys was greater when the preferred stimulus was in the receptive field (RF) and matched the previous cued feature. Notably, the neural response to distractor containing the preferred colors and cued (attended) was significantly enhanced regardless of their location in the visual display. These findings suggested that feature-attentional bias in favor of neurons with feature preference when matching the searched feature spreads throughout the visual field in parallel.

Treue and Martinez-Trujillo (Treue & Martinez-Trujillo, 1999) showed that the response of neurons in the MT region increased with attention (heights of tuning curves but not width). Such increment followed a multiplicative factor when the attended stimulus was inside of the RF of a neuron (attended -in). A more relevant effect was the increment of neural response when attention was switched between overlapping dots groups moving in different directions without changing the attended location and without changing the stimulus inside of the RF. It was observed then, that that the response of neurons increased while attending the preferred direction even though the attended motion direction was attended outside of the RF of the recorded neuron. Thus, when the preferred direction of neurons aligned with the attended direction, there was a general enhancement of the firing response and a reduction of the response of those neurons preferring the opposite direction (Treue & Martinez-Trujillo, 1999). Based on this seminal work, the Feature Similarity Gain Model (FSGM) was formulated. It states that attention changes neuron's responses in a multiplicative way such that the sign and strength of the modulation reflect the similarity between the attended feature and the neuron's feature preference (Martinez-Trujillo & Treue, 2004, 2005; Maunsell & Treue, 2006; Mcadams & Maunsell, 2000; Treue & Martinez-Trujillo, 1999).

Behavioral studies in humans have also documented the global nature of feature-based attention. Saenz and coworkers (Sàenz et al., 2003) showed that the task's accuracy improved when the feature (color/motion direction) presented at an unattended location was the same as the attended feature at the attended location. Saenz and coworkers (Sàenz et al., 2003) asked subjects to perform a speed discrimination or luminance discrimination task while two patches of dots moving upwards or downwards in both visual fields (left/right) were presented or varied the colors (red/green) of dots respectively. Behavioral indices of the spread of FBA effects throughout the visual field have been observed for orientation and motion. In these studies, the attention-induced aftereffects were used: TAE for orientation (Tilt After Effect relative to the vertical), and MAE for motion (Motion direction aftereffects). The FBA effects were tested at three locations varying in eccentricity from the adapter (center) for orientation (Liu & Hou, 2011) and motion direction (Liu & Mance, 2011). Similar sizes of FBA effects were found regardless of the distance between the adapter stimulus and the subsequent test-stimulus (eccentricity).

Saenz and coworkers (Saenz et al., 2002) using the same experimental design as (Sàenz et al., 2003) tested the BOLD response associated with GFBA. Selective neural modulations for color or

direction movement were observed in contralateral regions to unattended locations when the color (V4) or direction of movement (MT) was the same as the attended feature in the attended location.

Recent empirical evidence using Event-Related Potentials (ERPs) and Event-Related-Magnetic Fields (ERMFs) in humans have documented GFBA effects for color (Andersen et al., 2013; Bartsch et al., 2015, 2018, 2017; Moher et al., 2014; Zhang & Luck, 2009), orientation (Bondarenko et al., 2012) and motion direction (Stoppel et al., 2012). The classical experimental set up used in these studies was the "unattended probe paradigm," which is similar to the one used by Martinez-Trujillo (Treue & Martinez-Trujillo, 1999) and Saenz et al., (Saenz et al., 2002; Sàenz et al., 2003). It typically consists of two stimuli simultaneously presented one on the left and other on the right side of the visual field. One is attended (target), and the other is not (probe). Subjects are instructed to attend one feature value within the attended location to perform a task (target detection/discrimination). The stimulus in the unattended visual field contains either the attended or unattended feature value, but it is task-irrelevant. Neural responses are analyzed by comparing the elicited response by the probe for the attended relative to the unattended feature value (attended vs. unattended or Match vs. Non-match target feature) (see figure 3.4 in methods section for additional details).

While GFBA effects seem to be generalizable effects for several feature dimensions such as color, orientation, and motion-direction, there are still some characteristics not fully understood yet. One regards the timing of modulations, and a related is the stage of processing they first appear in the visual system. Observations by Zhang & Luck (2009) and Moher and coworkers (Moher et al., 2014) suggest that global color-based attention (GCBA) modulates the ERP response as early as ~100ms after stimulus onset (when the P1 component arises), suggesting an influence already on the initial feedforward sweep of processing. Notably, such early GCBA modulation (~100ms) was only visible when both colors (red/green) were presented together in the focus of attention (FOA) (Experiment 2: Zhang & Luck 2009 and Experiment 1: Moher et al., 2014). But not when they were presented sequentially (Experiment 3; Zhang & Luck 2009). Thus, the authors concluded that GCBA effects were the result of color competition in the FOA, and that is the cause for an early influence on the feedforward processing in the visual cortex (Zhang & Luck, 2009). Additionally, an extension of the work of Zhang & Luck 2009 by Moher et al. (2014) suggests that the actual mechanism underlying global color-based attention effect may be a relative inhibition of the unattended color in the FOA rather than an enhancement of the attended color (Moher et al., 2014). As yet, the debate about the nature of the ERP effect indexing GCBA is unsettled.

Other studies using a different experimental approach with color-probes testing the processing of attended feature with and without color competition, did not find early effects. Instead, late GCBA effects were documented (Bartsch et al., 2015, 2018). Bartsch et al. (2015) used two-color circles presented simultaneously in the left and right visual field for 300ms. The circle on the left side was attended, whereas the circle on the right side was not attended. The color competition was manipulated as follows: *Color competition*: Two different colors (red, green, for example) were presented simultaneously in the attended circle (target and distractor; experiment 1 Bartsch et al., 2015). *No-Color competition:* only one half of the circle was colored with the target color (Experiment 2 Bartsch et al., 2015). The main results showed that late GCBA responses (> ~160ms) appeared independently of whether the target color was presented with or without the distractor

color in the focus of attention, suggesting therefore that color competition was not needed for GCBA effects.

Additionally, global color-based selection (GCBA) was observed to be associated with two sequential amplitude modulations in the N1 and N2 time-range. The first one showed a maximum peak of around ~200ms (N1) and reflected a "template matching" process (Bartsch et al., 2015). A source localization analysis revealed that this modulation took place over the contralateral region to the probe (unattended stimulus) in the lateral occipitotemporal cortex. The second amplitude modulation reported by Bartsch et al. (2015) appeared later with a maximum peak at ~280ms (N2). It was named the "discrimination matching" effect, as it reflected the similarity between the probe color and the target color presented in the attended circle. The source localization analysis of the discrimination matching effect was contralateral to the probe in the posterior occipital region (Bartsch et al., 2015). Notably, Bartsch and coauthors (Bartsch et al., 2015) found that the early GCBA modulation (N1-range) appeared even when a currently target-defining color was not displayed in the attended location (Experiment 3; cross-match effect). And more importantly, it appeared in conditions without color-competition (Case 2, Experiment 2), i.e., when the attended color was presented alone with no distractor color displayed in the FOA.

Bondarenko reported similar results in the orientation domain (Bondarenko et al., 2012). The parametric manipulation of the unattended stimuli orientation relative to the attended stimuli orientation was observed for the N1 response (~150-200ms). In contrast, such variation relative to the stimulus orientation in the focus of attention (discrimination matching) was observed for the N2 response (~230-330ms).

Nevertheless, it is critical to mention that early studies using ERPs did not find clear support for global effects of color and motion selection when stimuli were briefly and unilaterally flashed (32ms) outside of the spatial FOA. As expected, significant spatial attentional effects were found as enhancements of the amplitude of P1, N1, and N2 components (attended vs. unattended). And later, color and motion selection effects for both features (N150-350) only when they appeared in the attended location (Anllo-Vento & Hillyard, 1996; Hillyard & Münte, 1984). In these studies, FBA effects were more prominent in the ERPs components beginning after 150ms in posterior regions and depicted as a negative deflection in agreement with the Selection Negativity (SN) concept (Harter, Aine, & Schroeder, 1982; Harter & Aine, 1984).

1.4 Object-Based Selection of Attention

In addition to spatial and feature-based selection, objects as a whole can serve as a reference frame of attentional selection. This phenomenon has been documented in psychophysical experiments (Baylis & Driver, 1993; Duncan, 1984; Egly, Driver, & Rafal, 1994; Lamy & Egeth, 2002; Valdes-Sosa, Cobo, & Pinilla, 1998), in single-unit recording studies in monkeys (Fallah, Stoner, & Reynolds, 2007; Katzner, 2009; Roelfsema, Lamme, & Spekreijse, 1998) and also with neuroimaging and electrophysiological recordings in humans (Boehler, Schoenfeld, Heinze, & Hopf, 2011; O'Craven, Downing, & Kanwisher, 1999; Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998).

Object-based selection describes the prioritization that attended objects acquire over the unattended ones. This effect is associated with the facilitation of all features/spaces appearing within the attended object boundaries relative to other unattended objects (Egly et al., 1994; Lamy & Egeth, 2002). Importantly, object-based selection requires object integration (integration of features defining the object) rather than the pure perception of single features without connectedness or grouping between them.

Experimental evidence for object-based selection is abundant. For example, there is the "same-object advantage," which refers to the observation that attending one feature of an object facilitates the processing of other features of the same object regardless of their task-relevance (Baylis & Driver, 1993; Duncan, 1984). This facilitation effect has also been observed when the spatial location is controlled so that the two objects: attended and unattended are in the same location (Blaser, Pylyshyn, & Holcombe, 2000; Valdes-Sosa, Cobo, et al., 1998). For example, indices of object-based selection have also been documented with ERPs by Valdes-Sosa and coworkers (Valdes-Sosa, Bobes, et al., 1998). They reported that the amplitude of the P1 and N1 waves was significantly suppressed to unattended dot surfaces (object) relative to the attended ones. These results suggested that, at the neural level, there is a separable representation of attended and unattended objects, even though the stimuli forming the objects are the same and appear in the same location. This data also suggested that object-based selection occurs at very early stages of visual processing (roughly at ~100ms).

Roelfsema and coworkers (Roelfsema et al., 1998) recorded single neurons in monkeys performing curve tracing experiments. They observed that attending one curve enhanced the neurons' response in area V1 of the monkey relative to the response evoked by a distractor curve even when the two curves crossed each other. A similar enhanced response of the area V4 of the monkey was observed when the object was attended (tag by color) relative to when it was not (Fallah et al., 2007).

Additionally, Katzner (2009) reported that the selection effect from one attended feature (color) in an object (colored dots 'surface) transferred to another irrelevant feature (motion) in the same object. This transfer was indexed by an enhanced response in MT (selective for motion) while attending the color of the moving dots. It seems that the integration of features forming an object allows transferring the benefits from one attended feature to the others in the same object. Object-based benefits were shown to even transfer to unattended objects containing unattended feature-values (color) of the attended object (Boehler, Schoenfeld, et al., 2011).

Furthermore, O' Craven et al.,(1999), using neuroimaging recordings (fMRI) in humans, showed that BOLD-signal increased selectively in the fusiform area when subjects paid attention to faces and in the parahippocampal place area when subjects paid attention to houses. MEG evidence has also supported these latter findings. Attention to faces versus houses enhances the response in the fusiform face area (FFA) and parahippocampal place area (PPA) depending on which object was attended (Baldauf & Desimone, 2014).

1.5 Computational approach for attentional feature selectivity: Selective Tuning Model (STM)

In computational modeling, visual attention is the critical mechanism required for visual selectivity. Vision is formulated as a search problem where, for any given stimulus, a subset of neurons best representing the input needs to be found (Tsotsos, 2005). There is common agreement among attention researchers that vision as a plain data-driven process is an intractable problem due to its combinatorial nature (Tsotsos, 1990). Thus, a selection mechanism that discards non-targets and optimizes search procedures becomes crucial (Koch & Ullman, 1985; Tsotsos, 2005).

One such model is the Selective Tuning Model (STM), which is a top-down model where the initial signals reach higher levels of processing to guide further processing. STM conceives of the visual systems as a pyramidal structure formed by a hierarchy of retinotopic areas (layers) receiving feedforward, feedback, and lateral connections on each layer (Tsotsos, 1999). STM is designed as a first principles model that takes into account the hierarchy and anatomical micro-circuitry of the visual system (Felleman & Van Essen, 1991).

According to STM, attentional selection requires two traversals of the pyramid. The first consists of representations of the interpretative units throughout the pyramid that are computed in a *feedforward* manner. The second is a Winner-Take-All process propagating in a reverse direction from the top down to the bottom layer of representation (inverse pyramid), thereby identifying the strongest item in each layer. On each layer, the process prunes away forward-projecting units, not contributing to the most salient item (Tsotsos, Culhane, Wai, Lai, Davis, Nuflo, 1995). The processes continue to find the winner at the next lower level – a process recursively applied in top-down direction throughout the visual system until the input layer is reached.

Some predictions derived from the STM such as the spatial profile of attention and feature-selection have been confirmed to have a center-surround shape (Boehler et al., 2009; Hopf et al., 2006, 2010; Störmer & Alvarez, 2014; Tombu & Tsotsos, 2008; Tsotsos et al., 1995; Wang, Miller, & Liu, 2015). For the color domain, in particular, some questions remain open. The global response pattern over the visual hierarchy is modulated by a selective tuning mechanism sharpening the response to target and presumably attenuating the response to nearby-to-target colors (Bartsch et al., 2017).

1.6 Reward-based biasing of visual selectivity

The reward is a powerful mechanism that modulates behavior at several levels. It does by increasing the probability of repeating behaviors linked to pleasant consequences (Schultz, 2006). Previous research has established that reward effects are mediated by dopamine release in the brain reward pathway (basal ganglia, *substantia nigra*, amygdala, dorsolateral and orbitofrontal cortices) (Schultz, 1998, 2000, 2007; Schultz, Dayan, & Montague, 1997). These dopaminergic neurons code detection, perception, and expectation of rewarding consequences (Schultz et al., 1997). Extensive research has shown that features, locations, and objects associated with reward improve task performance when they are targets or part of targets. In contrast, reward-associations with distractors impair

performance (less accuracy and longer RTs) (Anderson, Laurent, & Yantis, 2011; Chelazzi et al., 2014; Della Libera & Chelazzi, 2006, 2009; Hickey, Chelazzi, & Theeuwes, 2010a, 2010b; Kristjánsson, Sigurjonsdottir, & Driver, 2010; Theeuwes, 1994).

Data from several studies have documented that the size of reward (costs and benefits) modulates performance. The responses to high-rewarded items are faster and more accurate than the response to low-rewarded features or locations (Anderson et al., 2011; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a; Hickey, Chelazzi, & Theeuwes, 2014; Kiss, Driver, & Eimer, 2009; Serences, 2008; Stanisor, van der Togt, Pennartz, & Roelfsema, 2013). At the neural level, those reward benefits are reflected by activity changes in the visual cortical areas when animals (Arsenault, Nelissen, Jarraya, & Vanduffel, 2013; Baruni, Lau, & Salzman, 2015; Frankó, Seitz, & Vogels, 2010; Shuler & Mark, 2006; Stanisor et al., 2013) and humans (Baruni et al., 2015; Serences, 2008; Serences, Saproo, Serences, & Saproo, 2010) perform visual tasks. For instance, studies in humans reported that neurophysiological indices (ERP and ERFM) of attentional selection such as the N2pc component, (Eimer, 1996; Luck & Hillyard, 1994c) were speeded up and enhanced when reward-related features were defining the target in visual search (Buschschulte et al., 2014; Donohue et al., 2016; Harris et al., 2016; Hickey et al., 2010a; Kiss et al., 2009; Qi, Zeng, Ding, & Li, 2013; Sawaki, Luck, & Raymond, 2015). The response to unattended probes containing reward-related colors has been shown to increase, suggesting that rewarded features can bias the response in visual sensory cortices even though they are located outside of the focus of attention (Hopf et al., 2015). Similarly, neural responses varied as a function of reward size (high vs. low) and the probability of delivery (Arsenault et al., 2013; Buschschulte et al., 2014; Hickey et al., 2010a; Serences & Boynton, 2007; Stanisor et al., 2013; Weil et al., 2010).

The reward seems to modulate activity in the visual cortex in a very similar way as visual attention does. However, it is debated whether visual selectivity due to attention is simply guided by reward-associations (reward teaches attention, see below) or whether reward and attention operate independently in modulating visual cortical activity. This issue was raised first by Maunsell, back in 2004 (Maunsell, 2004), when he noticed that the experimental designs in animal research typically define attention via reward associations. Very similar effects of attention and reward would, therefore, be a trivial observation.

Nowadays, this debate still ongoing in the literature, even though more research has been done. On the one hand, experimental data is suggesting that attentional selection is guided (taught) by reward consequences. Thus, attentional resources are allocated strategically based on performance outcomes or according to implicitly learned reward associations, which consequently shape attention (Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Della Libera & Chelazzi, 2009; Della Libera, Perlato, & Chelazzi, 2011; Kristjánsson et al., 2010; Rombouts, Bohte, Martinez-Trujillo, & Roelfsema, 2015; Seitz, Kim, & Watanabe, 2009; Serences, 2008).

In contrast, other studies have shown that attention and reward do operate simultaneously in visual cortices, and independent top-down modulatory sources likely control them. Serences and Saproo (Serences et al., 2010) showed with fMRI in humans that the response to grating-orientations associated with reward in V1 varied as a function of the amount of reward independently of whether stimuli were attended or not. An fMRI study in monkeys showed that BOLD-signal varied (V3, V4, and TEO) as a function of reward in the absence of visual stimulation based on previously learned

reward associations (Arsenault et al., 2013). Similarly, Weil et al., reported that reward feedback after visual discrimination modulated the neural response in visual sensory cortices even when the reward was signaled as auditory feedback and the visual stimuli were not in the screen (Weil et al., 2010).

Nevertheless, to unambiguously verify that reward can bias sensory selection in visual cortices independently from top-down attention effects, it is critical to meet at least two requirements.

1) To separate operational definitions of task-related attention and reward contingencies, and 2) to independently vary one or the other influence. The first requirement of separating operational definitions of reward and attention has been already approached in recent studies by assigning different features (color/shape/objects category) or different feature-values to task-related associations and reward contingencies in visual search tasks (Buschschulte et al., 2014; Donohue et al., 2016; Hickey et al., 2010a) and color discrimination tasks using the unattended probe paradigm (Hopf et al., 2015). The second requirement will be addressed in the present work using versions of the unattended probe paradigm.

The unattended probe paradigm allows testing the reward and attentional accounts independently in the following way. The attended stimulus is presented in one visual field, the probe in the other visual field takes another feature-value associated with the target or with reward. Thus, the probe response elicited by each the reward- and attention-defining color can be tested separately. Additionally, the response to probes is orthogonal to the process of target discrimination, because "target discrimination" in the focus of attention is the same for all probe conditions. The advantage of this paradigm lies in the possibility of measuring the sensory bias elicited by different probe conditions, while target discrimination remains the same.

Hopf et al., (Hopf et al., 2015) used the unattended probe paradigm. The target location was fixed in the left visual field while the probe was located at the unattended side. The probe varied its color combination, either matching the target color, the reward color, the control color, or a combination of the target and reward color. This design allowed testing the response to target and reward probes independently of the response elicited by the target orientation-discrimination in the attended location. Interestingly, the results showed that reward-probes elicited a very similar response as the target probes in extrastriate visual cortices. Moreover, both responses were found to be additive when they were presented together. Thus, these findings suggest independence at the level of top-down influences on attention and reward.

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1.7 Influence of past selection history on ongoing visual selection

Effects of reward seem to be maintained for longer periods, potentially through a learned or an implicit feature-value association even when the reward contingencies have changed, and the past-reward features are no longer rewarded. These long-lasting reward-contingencies varied depending on the task. Previous research has been documented that reward-effects persist after weeks and even months when no other reward-associations are introduced (Anderson et al., 2011; Anderson & Yantis, 2013; Chelazzi, Della Libera, Sani, & Santandrea, 2011; Della Libera & Chelazzi, 2009; Hickey et al., 2010a, 2014; Hickey & van Zoest, 2013; Kristjánsson et al., 2010; Olivers & Hickey,

2010; Pollmann, Eštočinová, Sommer, Chelazzi, & Zinke, 2016; Sharifian, Contier, Preuschhof, & Pollmann, 2017).

Implicit feature biasing effects due to reward seem to resemble perceptual priming. Priming is an automatic process not affected by volition or conscious effort. Classical neuropsychological studies classified priming as part of the non-declarative (implicit) memory system emphasizing that it is a process out of conscious awareness likely operating at a pre-semantic level (Squire, 2004, 2009; Squire, Knowlton, & Musen, 1993) in a perceptual representation system (PRS) (Tulving & Schacter, 1990). Notably, perceptual priming is preserved in amnesic patients, it is not affected by development, aging, and drugs, and it is specific for the representation of primed items (Shimamura, 1986; Squire, 2004, 2009; Squire et al., 1993; Tulving & Schacter, 1990).

The literature distinguishes two types of priming: conceptual priming and perceptual priming. The first is more focused on lexical and semantic information and the latter on low-level stimulus properties processed in sensory systems (Schacter & Buckner, 1998; Wig, Grafton, Demos, & Kelley, 2005).

Perceptual priming typically generates facilitation effects in the form of shorter response times (RTs) to primed features relative to non-primed ones. These effects have been tested for colors, orientation, shape, motion (Becker, 2008b; Becker, Valuch, Ansorge, Mcdonald, & Fraser, 2014; Bichot & Schall, 1999, 2002; Eimer, Kiss, & Cheung, 2010; Goolsby, Suzuki, & Pace, 2001; Hickey, Olivers, Meeter, & Theeuwes, 2011; Maljkovic & Nakayama, 1994; Töllner, Gramann, Müller, Kiss, & Eimer, 2008), repeated locations (spatial location) (Maljkovic & Nakayama, 1996), faces, objects (Henson, 2003; Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004; Henson, Shallice, & Dolan, 2000; Müller, Gruber, & Keil, 2000) and also for more complex entities such contextual cueing (Chun & Jiang, 1998; Olson, 2001) and the size of the attentional focus (Fuggetta, Lanfranchi, & Campana, 2009).

While most of the studies have primarily focused on positive effects of priming (facilitation of perception, detection, discrimination, and remembering of the previous seen/attended items), priming can also have negative performance effects (negative priming). For example, negative priming appears as a slowed response (longer naming response time) to objects previously ignored relative to control and/or previously selected objects (Tipper, 1985, 2001). Such negative effects are believed to be part of an inhibitory mechanism acting on the internal representation to make the selection process more efficient (D'Angelo, Thomson, Tipper, & Milliken, 2016; Maljkovic & Nakayama, 1994; Neill & Valdes, 2004; Tipper, 2010).

Visual perceptual priming is a type of implicit short-term memory (Maljkovic & Nakayama, 2000; Schacter, 1987) driven and affected by repetition in a cumulative way. RTs of subsequent trials (priming facilitation) are inversely related to the amount of repetition of the same feature over trials. In visual search tasks (guided by color), this relationship follows an approximately negative exponential function. The facilitation effect persists for many trials, it has the largest effect for 5-to-8 consecutive repetitions, and typically reaches an asymptote after eight repetitions (Goolsby et al., 2001; Maljkovic & Nakayama, 1994, 1996). The pure repetition of items cannot fully account for the facilitation effects. Attentional deployment to those features (targets or distractors) is needed for

modifying their subsequent perception (Goolsby et al., 2001; Kristjánsson, 2006; Kristjánsson, Vuilleumier, Schwartz, MacAluso, & Driver, 2007; Tulving & Schacter, 1990).

Whether priming is selective to the attended feature or whether it affects all features of the attended stimulus is still debated. On the one hand, some studies have reported that for pop-out features (colors), priming is very features-selective with no transfer effects to other features of the target-stimulus. This effect remains even for features requiring discrimination and response-relevance, but they are not searched (Maljkovic & Nakayama, 1994). Other studies have found that perceptual priming works in a holistic fashion affecting all features of the target (Becker, 2008a; Huang, Holcombe, & Pashler, 2004), thereby weighting the magnitude of facilitation (larger effects for relevant than irrelevant features).

Electrophysiological studies have shown that color priming in visual search tasks modulates early ERPs responses including the P1 (Hickey et al., 2011; Olivers & Hickey, 2010) and N2pc waves (Eimer et al., 2010; Hickey et al., 2011; Olivers & Hickey, 2010; Töllner et al., 2008). Early responses are modulated by priming as a function of ambiguity (distractor presence and Target-Distractor similarity). In essence, the P1 is smaller in amplitude for repeated target colors relative to alternating target colors (Hickey et al., 2010a). The N2pc, in contrast, appears earlier and is larger in amplitude when the target color was repeated as compared to when it was not repeated (Olivers & Hickey, 2010). Similarly, in a rewarding context, the P1 and N2pc response for repeated target and reward-related colors was larger for high reward trials relative to low reward trials.

Moreover, priming effects of complex stimuli such as object drawings were characterized by reduced ERP amplitudes in the time range of 230-380ms (posterior electrodes) and 390-490ms (central electrodes) for primed versus non-primed images (Gruber, Malinowski, & Mu, 2004; Gruber & Müller, 2002).

In summary, priming effects vary with task demands and the type of stimulus used (Kristjánsson & Campana, 2010). They likely reflect neural changes in cortical modules involved in the analysis and processing of primed features, feature combinations, and objects (Magnussen & Greenlee, 1999; Schacter, 1987, 1990; Tulving & Schacter, 1990).

II. MOTIVATION

First experiment. This work focuses on mechanisms of global feature selectivity for color. Feature-based attention is a mechanism that operates in a spatially global manner so that relevant features located outside of the focus of attention (unattended locations) are also selected (Andersen et al., 2013; Bartsch et al., 2015; Bondarenko et al., 2012; Moher et al., 2014; Saenz et al., 2002; Sàenz et al., 2003; Stoppel et al., 2012; Zhang & Luck, 2009). Previous studies have reported that indices of global-color based attention appear as earlier as 100ms (P1 modulation in ERPs) and presumably influence the *feedforward* flow of visual information. This early modulation is thought to reflect a competition process between the attended and unattended color within the FOA either by a mechanism of enhancement of relevant color (Zhang & Luck, 2009) or by suppression of irrelevant ones (Moher et al., 2014). In contrast, other studies manipulating color competition in the FOA have not seen this early modulation; instead, they have described a sequence of modulatory effects appearing after ~150ms likely corresponding with feedback signals reflected by the posterior N1 and N2 components (Bartsch et al., 2015, 2018).

This apparent disagreement in the literature on the temporal dynamics of the GCBA effects has not been settled yet. It is not clear, however, whether the GCBA effect appears already during the feedforward sweep of processing in the visual cortex or as a consequence of feedback processing. One likely, yet untested, the possibility is that studies showing feedforward modulations (Moher et al., 2014; Zhang & Luck, 2009) used a continuous stimulus presentation protocol, where subjects continuously attended a stream of colors that presumably *preset* an early bias for the attended color. In contrast, studies showing exclusively feedback effects used a different protocol where stimuli appeared in a trial-by-trial manner such that on each trial, the attended color is *reset* from scratch requires more time to tune the system into the attended feature.

Here, GCBA indices are compared depending on whether color items in the attended location are presented in a trial-by-trial onset manner or whether they are continuously displayed while smoothly progressing through color space. The continuous color stream is continually driving the feedforward sweep of processing, which allows for an ongoing bias of selectivity that is refined (tuned) when the color stream approaches the target color. In the trial-by-trial onset condition, no such refined tuning is possible. The unattended probe paradigm was used as a general experimental approach (Bartsch et al., 2015, 2018, 2017; Bondarenko et al., 2012; Moher et al., 2014; Saenz et al., 2002; Sàenz et al., 2003; Stoppel et al., 2012; Treue & Martinez-Trujillo, 1999; Zhang & Luck, 2009). Two colored circles were used, one in each visual field, one being attended, and the other being unattended (probe). In the first condition, the attended circle is continuously displayed in the focus of attention while its color steadily progresses through color space. In the second condition, the attended circle is displayed for 300ms in a classical trial-by-trial onset manner followed by a blank period (see more details in the methods section of experiment 1). The same target colors, probe colors, timing, and order of blocks are used in both conditions. The only difference between them is the way the stimuli are presented at the attended location: continuous versus onset, with the former allowing to preset-bias the target color on each probe-presentation.

The main question is whether and how the GCBA response would vary depending on whether the attended color is presented in an onset trial-by-trial manner or in a continuous way that biases the visual system into the attended color continuously.

The second experiment tests the role of the degree of selectivity and tuning on GFBA. Previous studies typically use distractor colors, which differ substantially from the target and do not require fine color selectivity. Here, in contrast, it is evaluated whether GFBA reflects a selective tuning mechanism when the target color in the focus of attention is combined with a distractor color in the focus of attention that is similar to the target (labeled as Target-Distractors). According to the STM (Tsotsos, 2011; Tsotsos et al., 1995), attention sharpens the response to attended features by a top-down WTA process, which prunes away neural signals not representing the target. Thus, when the target color is presented paired with a very similar distractor color, the selectivity for the color likely increased by attenuating the neural response to non-attended colors. This attentional tuning mechanism for color selection would be reflected in the ERPs and ERMFs. Importantly, the attenuation would be expected to be the larger the similar the target and distractor color are. Alternatively, the increased color selectivity would not be attained through attentional tuning, with the GFBA response showing no attenuation.

To test the hypothesis, the response to probes matching the target color was compared while varying the similarity between the target (T) and distractor colors (D) in the focus of attention. For example, when the target is red, distractors appear in a purplish red closer or farther away from the target in color space. First, the target discrimination rate was individually adjusted to set distances between target and distractor (See Methods section for details); and later, the GFBA response was compared as a function of T-D similarity.

Experiment three focuses on the question to what extent GFBA and global reward-related responses (Hopf et al., 2015) refer to the same or separable biasing mechanisms in the visual cortex. Within the literature, there is a controversy regarding whether reward encourages attentional selection (Chelazzi et al., 2013; Della Libera & Chelazzi, 2009; Della Libera et al., 2011; Kristjánsson et al., 2010; Rombouts et al., 2015; Seitz et al., 2009; Serences, 2008), or whether reward associations modulate sensory selection independently of task-relations (Arsenault et al., 2013a; Buschschulte et al., 2014; Hickey et al., 2010a; Hopf et al., 2015; Serences et al., 2010; Weil et al., 2010). Previous work has shown that attention-related (GFBA) and reward-related colors elicit similar neural responses (same size, time course, and source localization) in visual cortices. And the modulatory responses of GFBA and global reward-based selection (GRBS) were almost additive when presented together (Hopf et al., 2015). Results from this study were taken to suggest that independent top-down modulatory sources might control reward and attention. But with the data at hand, the issue could not be settled. If it is the case that reward and attention dissociate at the top-down level, a selective variation of one modulatory factor should only influence the corresponding neural response in the visual cortex. In experiment three, this prediction is tested varying attentional load (load on GFBA), while simultaneously maintaining reward-related factors constant (constant GRBS) over the experiment. In the first part of experiment 3, the attentional load is varied to set comparable levels of difficulty for each subject. Later GFBA and GRBS related modulations are compared as a function of task difficulty (easy and hard).

Finally, **experiment four** explores the role of attention and reward priming on GFBA and GRBS. Several studies have shown that the acquired priority of the attended features and features related to reward persists many trials later (Becker, 2008b; Becker et al., 2014; Bichot & Schall, 1999, 2002; Chun & Jiang, 1998; Eimer et al., 2010; Goolsby et al., 2001; Henson, 2003; Henson et al., 2004; Henson et al., 2000; Hickey et al., 2010a, 2011; Kristjánsson, 2006; Kristjánsson, Ingvarsdöttir, & Teitsdöttir, 2008; Kristjánsson et al., 2007; Maljkovic & Nakayama, 1994, 1996; Müller et al., 2000; Olson, 2001; Töllner et al., 2008). This prioritization appears as speeded RTs to targets, and amplitude changes of early and later ERPs components reflecting attentional selection (P1, N2pc) of the target (Eimer et al., 2010; Gruber & Müller, 2002; Hickey et al., 2010a, 2011; Olivers & Hickey, 2010; Töllner et al., 2008). Currently, it is unclear whether these priming effects reflect a plain global feature-based bias or a more item-related selection bias. The unattended probe paradigm provides the advantage to test this possibility directly because neural responses to primed-, match, or control features can be measured independently. Furthermore, it allows assessing whether priming effects of reward and attention dissociate.

III. GENERAL METHODS

3.1 Subjects

Participants in the experiments reported here were students from the Otto von Guericke University of Magdeburg community. They gave their informed and written consent and were paid for their participation (6-8 € per hour). All subjects had normal or corrected to normal vision and no report of neurologic diseases. The number of participants is described in each experiment section.

3.2 Experimental design

The series of experiments reported in this work investigates the mechanisms of global feature selectivity. To this aim, the unattended probe paradigm was used as a general approach with variations in stimulus features and task instructions on each experiment. As seen in figure 3.1, the unattended probe paradigm consisted of two stimuli displayed in the lower quadrants of the visual fields: the stimulus placed in the lower-left visual field (LVF) was designated as "attended stimulus" because it contained the task-relevant feature (TARGET). In contrast, the stimulus displayed in the right visual field (RVF) was the unattended stimulus labeled as PROBE-stimulus (probe in the following text). The probe varied in feature values so that in some trials the probe matched the attended feature (Match trials =M), while in another did not (Non-Match trials =NM). Importantly, the probe was always irrelevant to the task.

On each trial, subjects were asked to fixate a central cross and covertly attend the "attended stimuli" to perform the discrimination or detection target task, while ignoring the probe in the right visual field. Global feature selectivity indices were obtained by comparing the response to the probe as a function of whether it matches the attended feature or not (Match Target = M [dark blue

lines] versus Non-Match Target= NM [green lines]). Thus, the GFBA index used here is the response difference match minus non-match trials (M-NM) shown in lilac in figure 3.1.

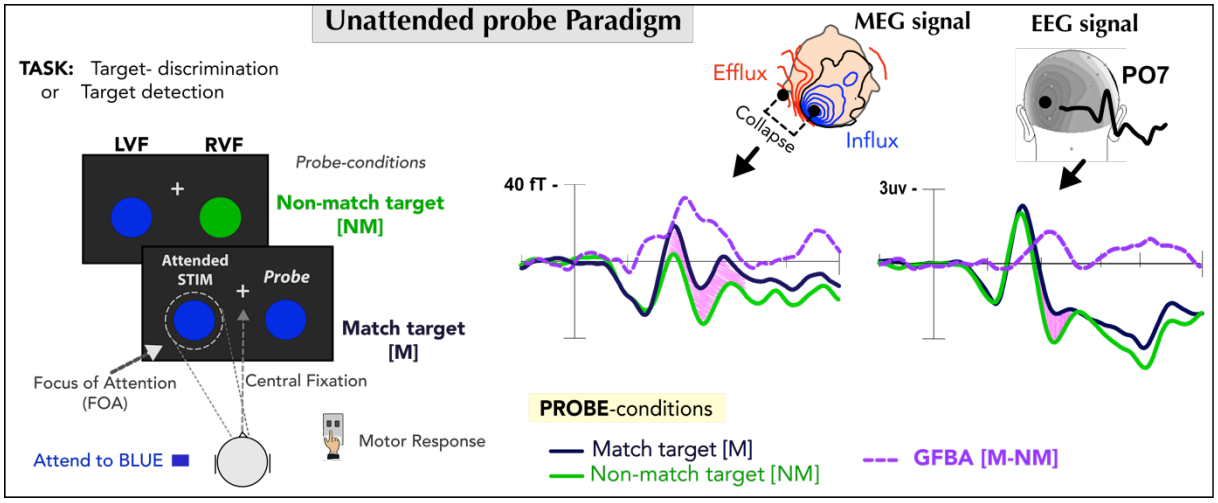

Figure 3.1. a) Schematic illustration of the unattended probe-paradigm. The task consists of detecting or discriminating the target color in the focus of attention. Global feature-based selection is indexed by the difference response between two probe-conditions: match target (dark-blue lines) minus non-match target (green lines) trials; GFBA =M-NM is plotted in lilac lines.

3.3 Stimuli

Stimulus features varied accordingly to the purpose of each experiment; on the methods section of every experiment, there is a detailed description of them and the reasoning behind. Stimuli were created and presented in the back-projected screen in the MEG room using MATLAB release 2009b, The Mathworks, Inc., Natick, Massachusetts, United States, and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

3.4 Data acquisition

Brain signals were acquired by recording the magnetoencephalogram (MEG) and the electroencephalogram (EEG) simultaneously. The EEG system (Neuroscan Inc., Herdndon, VA) consisted of 32 channels (Easycap GmbH, Herrsching, Germany) placed according to a modified version of the 10/20 system (Böcker, van Avermaete, & van den Berg-Lenssen, 1994). The *Fpz* electrode was used as the ground (Figure 3.2). Eye movements were monitored using an EOG arrangement consisting of 2 electrodes located at the external ocular canthi of each eye for horizontal movements (HEOG, bipolar) and a vertical electrode placed below the right eye for vertical motion (VEOG, monopolar). Electroencephalographic signal was online referenced to the right mastoid (bony protrusion behind the ear) and offline re-referenced using the average of the left (Lm) and right mastoid (Rm) reference ([Lm + Rm)] /2) (Luck, 2014). Electrode Impedances for all channels were kept below five kΩ through each experiment.

The magnetoencephalogram for experiments 1,2 and 3 was recorded using a 4DNeuroimaging MEG scanner. It consisted of 248 magnetometers, as seen in the middle figure 3.2, covering the whole head (BTI system, Magnes 3600 WH, San Diego, CA, USA). The MEG signal was online filtered with a band-pass filter from 0.01- 100Hz and digitized at a sampling rate of 508.6 Hz. Noise cancellation for data collected with the 4D Neuroimaging scanner was done online by mean of an array of reference coils located within the system but further away from measurement sensors to record the external noise. Later, such noise was subtracted from the MEG primary sensors output (Robinson, 1987; Vrba & Robinson, 2001).

Experiment 4 was recorded using an Elekta Neuromag® TRIUX™ MEG scanner consisting of 102-sensor triplets, as seen on the right side of figure 3.2. Each triplet has one magnetometer and two orthogonal planar gradiometers (102; 204). The continuous MEG signal was online filtered with a band-pass filter of 0.01- 300Hz and digitized at a sampling rate of 1000 Hz. (During offline preprocessing, data was down-sampled to 500Hz). Environmental noise was canceled by applying the signal space separation method [SSS method (Taulu & Simola, 2006; Taulu, Simola, & Kajola, 2004)] implemented in the Maxfilter™ v. 2.2 software (Elekta Neuromag). SSS is a method that utilizes the fundamental properties of the electromagnetic fields and harmonic function expansions to separate the measured MEG data into three components: brain signals, external disturbances and noise and artifacts close to sensors. SSS applied the Maxwell equations to remove the component of magnetic fields originated from outside the MEG helmet (Elekta Neuromag® TRIUX™ MEG-Handbook 201x).

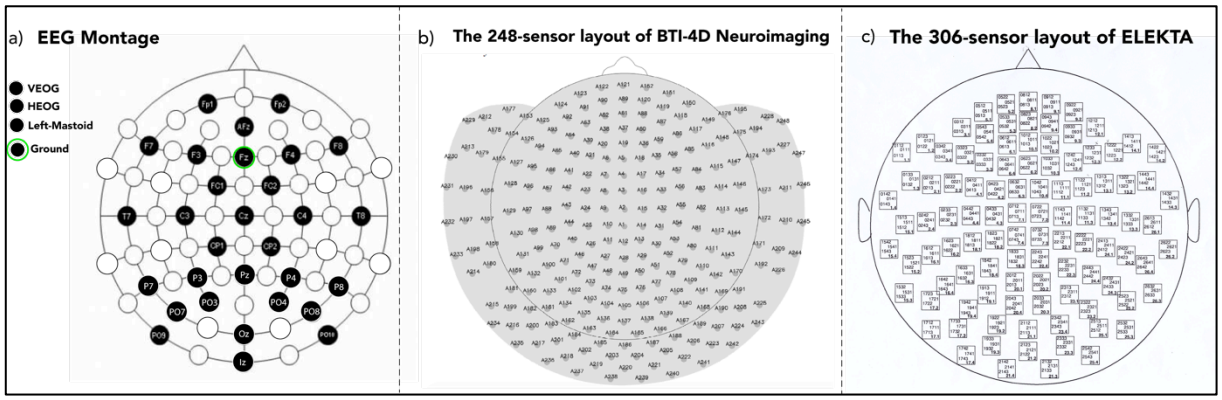

Figure 3.2a shows the EEG-Montage (a) formed by 32 electrodes, including the EOG electrodes to record Vertical (VEOG) and Horizontal (HEOG) eye movements. Layout taken and modified from https://www.easycap.de/layouts/ B illustrates the 248-layout of the BTi 4D Neuroimaging system. C shows the layout of the 306 sensors of the ELEKTA scanner. The layout took and modified from https://www.elekta.com/diagnostic-solutions/elekta-neuromag-triux/

The head subject's position was online monitored using an infrared camera. When subjects moved from their starting position, they were instructed to return to it. Before MEG-EEG recordings, data from the head position of subjects were acquired by using the Polhemus 3Space Fastrak digitization

system (Polhemus Inc., Colchester, VT, USA). The position of five markers coils placed at standardized locations in the EEG-cap, as well as the EEG-sensors location, was taken.

3.5 Preprocessing of electrophysiological data

MEG and EEG signals were offline epoched, including a 200ms baseline period before and 700ms window after stimulus onset. Epochs were visually inspected and submitted to artifact rejection to remove noisy trials containing eye blinks, eye movements (horizontal and vertical), muscle or heart artifacts, and environmental noise.

Artifact rejection was done as follows: For data collected with the 4D Neuroimaging MEG scanner, the signal was first visually inspected. Then artifacts were offline identified using a peak-to-peak threshold criterion: MEG (range=2.8 -3.9 fT) and EEG signal (range=80 - 130uv) individually adjusted. Data collected with Elekta Neuromag® TRIUX™ MEG scanner was offline preprocessed first using the signal space separation SSS Maxfilter™ Tool implemented by ELEKTA for noise cancellation and then submitted to artifact rejection using fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The *ft_define_trials* and *ft_preprocessing* functions from fieldtrip were used to define trials and epoch data [-200,700ms]. Then, the *ft_artifact_zvalue* function and its graphical interface were used to detect and visually inspect artifacts for each epoch and channel. The *ft_artifact_zvalue* function transforms the amplitude of the signal over time (The Hilbert envelope), calculates a z-normalized-score (mean subtracted and divided by standard deviation) for every time-point, and then averages these z-values. Averaging z-values over the type of sensors have the advantage of evidence artifacts-accumulation over sensors (neighbors usually). A threshold (z-value) was established for the global *z score*. The fraction of epochs with deviations above the threshold, at any time point of interest, were marked to be discarded. (*ft_artifact_zvalue*; http://www.fieldtriptoolbox.org/reference/ft_artifact_zvalue/). This step was repeated for muscle artifacts, jumping channels, and ocular movements. Artifact rejection was run independently for magnetometers and gradiometers.

A similar process was applied for muscle artifacts and ocular movements for the EEG signal. While a different set of parameters specifying subsets of channels, filtering bands, type of padding, and *z*-score amplitude thresholds were used, default parameters were used for all subjects. Amplitude thresholds (cutoff values) were adjusted iteratively, trying to maximize the rejection of noisy epochs while preserving the maximum number of accepted trials. MEG and EEG data were low-pass filtered (to 30Hz) using the *ft_preproc_lowpassfilter* Fieldtrip Toolbox function (Butterworth IIR filter; two-pass filter direction: zero-phase forward and reverse filter).

ERPs and ERMF average-waveforms were computed time-locked to probe onset (unattended stimuli) according to probe conditions. Only trials with correct responses were included. Waveforms were averaged and plotted using ERPSS software (Event-Related Potential Software System, University of California, San Diego, La Jolla CA, USA) and Fieldtrip Toolbox for data collected in Elekta Neuromag® TRIUX™ MEG scanner.

3.6 Alignment of individual head positions (repositioning MEG data)

Although the head's subjects' position was monitored online, subjects might have different positions within the MEG helmet during recording. These differences are millimetric, but they might be a source of smearing out true effects due to the brain areas of interest that might have been measured by different neighboring sensors across subjects. Such differences between individual data sets can be treated, in principle, using a method to align individual head positions to a standard reference. Before averaging data across subjects for experiments recorded with a 4D Neuroimaging scanner (Experiment 1,2, and 3), we run a custom routine to align individual head positions. Running this procedure requires to have *reference-sensor position* data. The common *reference -sensor position* is the representation of the most canonical sensors position respect to the landmarks (In data collected with 4D Neuroimaging MEG scanner; Sensors A214, A226, A121, A1, and A220 correspond to left and right preauricular, nasion, central and inion respectively). The common *reference-sensor position* was derived from a subject with the minimal difference respect to the computed mean values of 1500 MEG recordings in our lab (Unpublished data/Department of Neurology, 2013).

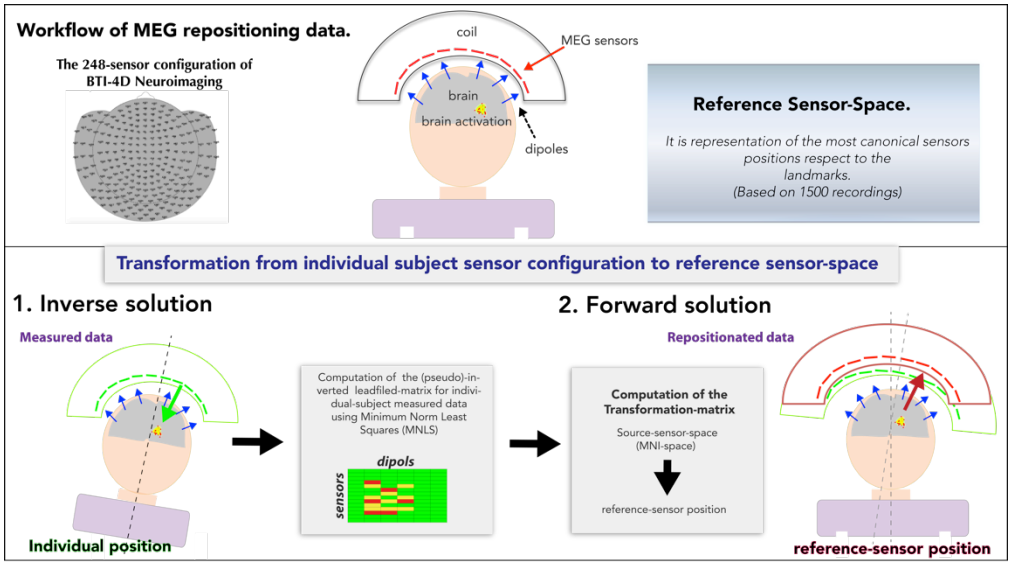

Figure 3.5. It describes the workflow of the MEG repositioning data process. The transformation from the individual subject sensor to reference-sensor space had two main steps: Inverse solution and Forward solution.

Computing the linear transformation from individual original sensor-position to the reference sensors position consisted of two steps, as we see in figure 3.5. I) *Inverse solution.* This step transforms data from individual sensors space into the MNI-source space. The lead field matrix was (pseudo)-inverted using the inverse solution MNLS method Minimum Norm Least Squares) (Fuchs, Wagner, Köhler, & Wischmann, 1999). Computation of individual (subject-by-subject) leadfield matrix describing a dipole for each sensor was done using Curry 7.1 Neuroimaging Suite (Neuroscan, Charlotte, NC, USA). The MNI standard brain template (Montreal Neurological Institute, ICBM-152 template) was used as a source space and volume conductor model.

II) *Forward Solution.* This step consisted of computing the Transformation Matrix that brings the data from MNI-source space into the reference sensor position.

A measure of goodness of transformation based on the variance between the original and reference data was also calculated. When the variance was high (square-root-of factor of variance-change > 2) data-subject were excluded from the grand average.

3.7 Statistical analysis of data

Arithmetic means and standard errors of correct response time (RT in milliseconds) and the proportion of correct responses (percentage) were calculated. Incorrect responses or responses that occurred sooner than 200ms after stimulus onset were excluded.

Behavioral data analysis was performed as follows: first, repeated measures analyses of variance (ranova) were computed separated for accuracy and response time. Ranova designs were adjusted on each experiment according to the design. Whenever the ranova tests were significant, *posthoc* pairwise comparisons were performed using paired sample t-test between probe-conditions. Bonferroni correction for multiple comparisons was used for adjusting the alpha-level in the posthoc analysis.

Statistical analyses of electrophysiological data were performed at the sensor level. For the EEG signal, we selected the PO7 electrode located contralateral to the probe. PO7 was chosen because it captures the response in visual areas elicited by the probe presented in the left visual field due to the retinotopic organization of the visual cortex as previous studies in our group have shown (Bartsch et al., 2015; Bondarenko et al., 2012).

For the MEG signal, as the magnetic field is a complex signal described by two components: efflux (+) and influx (-), the selected sensors are those showing the local maximum of the efflux (red) and influx (blue) at the posterior region contralateral to the probe (see figure 3.4). As we see in figure 3.4, the waveforms correspond to the collapsed signal at the sensor level. This collapsed signal is computed by averaging the efflux (red) and influx (blue) components after reversing the polarity of the efflux to avoid cancellation. This computation was performed for each experimental condition of interest on the average condition response across trials per subject. Thus, the statistical analysis was performed on the collapsed waveforms of single subjects.

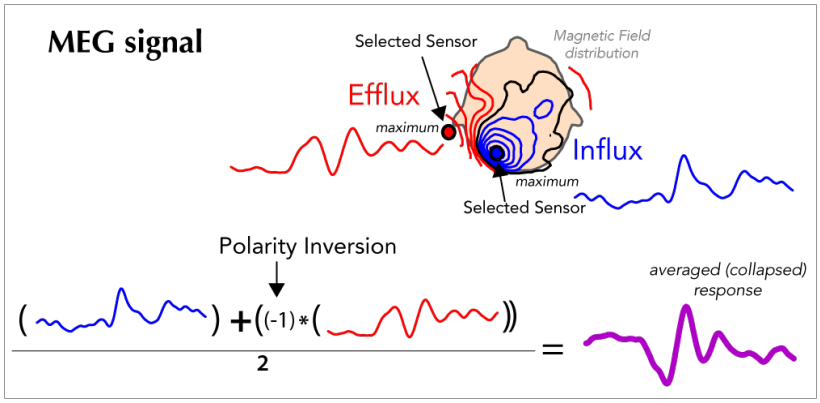

Figure 3.4 a) Schematic illustration of the computation of collapsed waveforms by averaging the efflux in red lines and influx in blue lines of the magnetic field after reversing the polarity of the efflux (red lines) to avoid cancellation. The averaged (collapsed) response in purple is the magnetic response for each condition of interest on each subject. This collapsed response was submitted to statistical analysis.

Repeated measures analyses of variance (ranova) were computed using the ERPSS software (Event-Related Potential Software System, University of California, San Diego, La Jolla CA, USA) for the neurophysiological signal. Greenhouse-Geisser correction for violation of sphericity was applied when it was needed. A time-sample-by-time-sample sliding window approach was used to determine the onset of the significant effects. Mean amplitudes were taken over successive intervals (10-30ms, step size = 2 samples) and tested for significant differences between conditions. A p-value < 0.05 was established as a criterion to reject the null hypothesis. To control for increasing error type 1, only when five consecutive intervals reached statistically significant values were considered as valid significant effects (Guthrie & Buchwald, 1991). All statistics were performed on unfiltered data, but for the visualization of waveforms, a Gaussian smoothing filter was applied (time-domain SD of 2 or 4 sample points).

3.8 Current sources estimates

Source analysis of the grand average was computed using the MNLS method (Minimum Norm Least Squares) (Fuchs et al., 1999) implemented in Curry 7.1 Neuroimaging Suite (Neuroscan, Charlotte, NC, USA). The MNI standard brain template (Montreal Neurological Institute, ICBM-152 template) was used as a source space and volume conductor model.

IV. EMPIRICAL WORK

Part 1. Neuromagnetic indices of global feature selection in the human visual cortex

4.1 Experiment 1

Feature attention enhances the representation of relevant features in a global manner throughout the visual field regardless of their locations. Whether global color-based attention effects appear at early (~100ms) or later stages (~160-200ms) in the visual processing is something still in debate. Previous studies have shown that GCBA can influence the *feedforward* sweep of visual processing (Moher et al., 2014; Zhang & Luck, 2009), while others studies have documented that GCBA only modulates the later responses (feedback signals) (Bartsch et al., 2015, 2018). The fact that stimuli in those studies were differently presented in the focus of attention either in a classical onset-trial-by-trial or in a continuous way suggests that stimulus-presentation type might play a critical role. Because it allows *presetting* and *upholding* target color information, contrary to when stimuli are presented onset trial-by-trial, which resets the attended state (resetting condition). Therefore, this experiment compares the GCBA indices as a function of the way stimuli are presented in the focus of attention (continuous versus trial-by-trial onset).

4.1.2 Subjects

Twenty-seven students (mean age= 26.44 $\pm$ 3.60, range 21 to 33 years old) at the Otto-von-Guericke University of Magdeburg participated in the experiment. All participants were right-handed, had normal or corrected-to-normal vision, and 8 of the total were women.

4.1.3 Stimuli

Two full-colored circles were displayed on the lower quadrant of each visual field in a gray background (lum=10.6 cd/m^2). The circle on the left visual field was the attended stimuli, whereas the circle presented at the right visual field was the unattended stimulus or probe (irrelevant for the task). Both the attended and unattended stimuli were circles full filled with red, green, or blue colors (figure 4.1a).

All colors used were taken from the HSV space. The Hue-saturation-value (HSV) coordinate system is a cylindrical space described by three parameters: Hue (0°-360°), Saturation (radial measure), and Value (z-height). The HSV space color has the advantage that its contours are constant and perceptually linear. By fixing S and V, Hue cyclically rotates through the color with a fixed level of "light," and by setting H and S, Value goes from full black to full color (figure 4.1b). Color values of stimuli were taken from HSV color coordinates and then translated into RGB values to be displayed on the screen.

Two stimuli presentation types were used: continuous and onset trial-by-trial. In the *onset* condition, the stimulus (colored circle) in the attended location was presented by 300ms and then followed by a blank (Inter stimuli interval= 800-1200ms) so that the onset and offset of the circle were clearly perceived. The *continuous* condition, in contrast, was similar to the *onset* condition in timing: attended stimulus = 300ms and ISI = 800-1200ms, but with the difference that during the Inter stimulus Interval, a continuous stream of colors was presented in the attended location circle. The color stream

was progressively going from one cardinal to another color through intermediate values within the color space, as we see in figure 4.1b. The intermediate colors were presented for a very short time without space in between promoting the perception of a continuous stream at the attended circle location (figure 4.1d). For example, when the previously attended stimulus was red, and the next cardinal color at the attended circle was blue. The continuous stream went progressively through several levels of red-magenta, pink, and violet until it reached the attended blue.

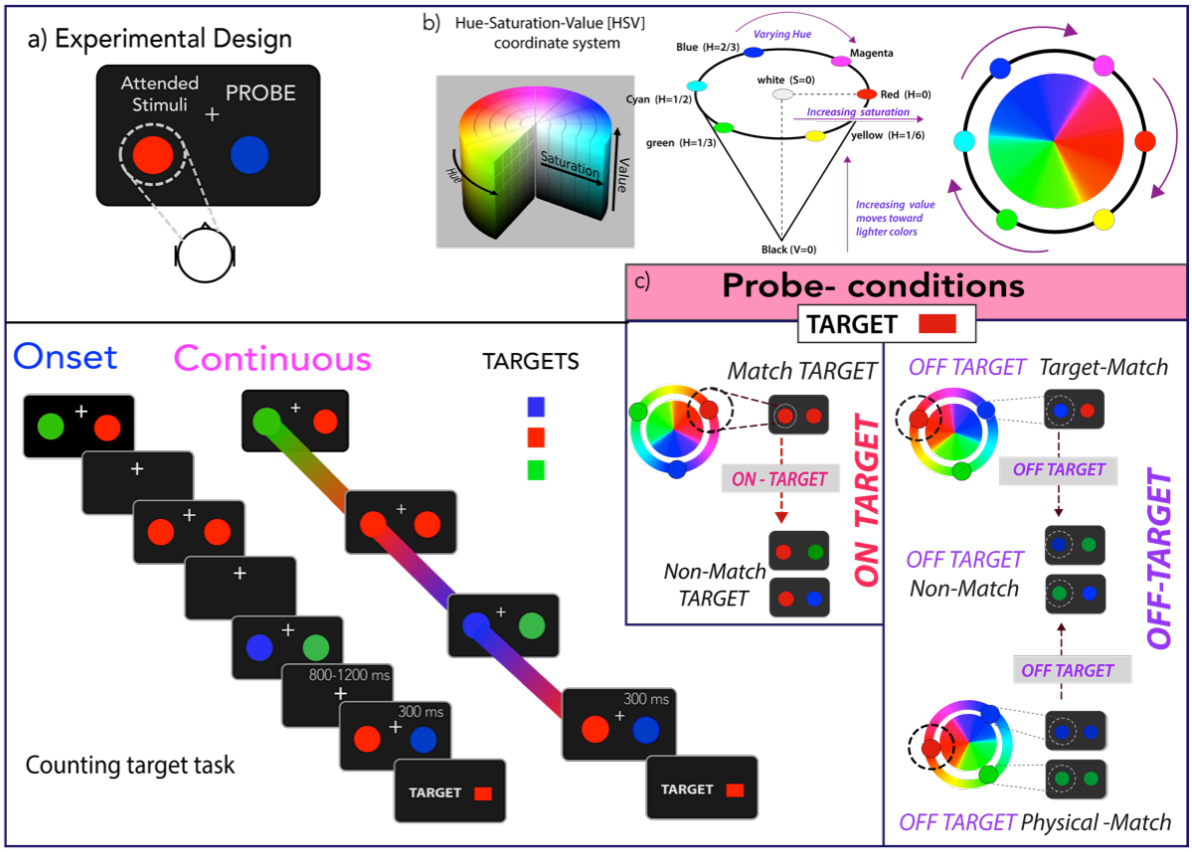

Figure 4.1 Experimental design. a) Schematic illustration of stimuli: The attended circle was displayed on the left visual field and the unattended on the right visual field. For illustration, red is used as the TARGET, but red, green, and blue colors were used as the target over the experiment. There were two stimulus-presentations: Onset and Continuous: the critical difference between them was the continuous stream of color presented during the ISI in the continuous condition in the attended stimulus. b) Probe-conditions were organized according to the colors in the probe (Match vs. Non-Match the current target) and whether TARGET color was or not on the attended circle (ON-TARGET and OFF-TARGET respectively).

Target colors (red, green, and blue) lasted 300ms when they were in the attended location, and their frequency of presentation was equally distributed. The direction of the continuous stream within the color space was randomized and equally probable. Therefore, when the last color from the attended location was blue, for example, the next cardinal color could be red or green with the same probability in the current and the subsequent trials avoiding predictability on the direction of the continuous stream.

The unattended circle located in the right visual field was colored in red, green or blue, and displayed by 300ms followed by a blank period (800ms-1200ms) in the *continuous* and *onset* conditions. Probe and attended circles (red, green, blue) were both concurrently presented in continuous and onset conditions.

This experimental design allowed us to form the following probe-conditions: Match and Non-match Target. Additionally, these trials were divided into two categories: ON-TARGET and OFF-TARGET, depending on whether the attended color was or was not in the attended circle. There was another type of trial where both colors in the displayed circles (attended circle and probe) were the same (OFF-target physical match) but not the current target color. In total, five probe-conditions were formed: ON-TARGET-Match, ON-TARGET-Non-Match, OFF-TARGET-Match, OFF-TARGET-Non-Match, and OFF-TARGET-physical_match (see figure 4.1).

Trials were blocked by target color and stimuli-presentation having in total 24 blocks. Twelve blocks were continuous, and 12 were onset type. The order of color and type of stimuli-presentation was interleaved: continuous red, onset green, continuous blue, onset red, continuous green, onset blue, and so forth until the 24 blocks. No immediate repetition of attended color or stimuli-presentation type between contiguous blocks happened.

4.1.3 Task

Subjects were instructed to fixate at the central fixation cross and covertly paying attention to the stimuli presented in the attended side (left visual field) while ignoring the stimuli at the right visual field (unattended stimuli). On each block, one color was designated as the target, and subjects had to count the number of times this target color appeared in the attended circle (left visual field =LVF). After completing each block, subjects reported their response verbally and received feedback about their performance.

4.1.4 Data recording and statistical analysis

EEG and MEG signals were epoched using 200ms as baseline and 700ms following the stimuli onset. Epochs with recording, motion artifacts, eye blinks and eye movements were excluded using a peak-to-peak threshold criterion for MEG (M= 3.35 fT, SD=0.32fT, range= 3 -3.9fT) and EEG (M=117uv, SD= 8.7uv, range= 110 - 135uv) signal. Grand averages were calculated according to probe-conditions: ON-TARGET-Match, ON-TARGET_Non-Match, OFF-TARGET-Match, OFF-TARGET-NonMatch, and OFF-TARGET-physical_Match.

Statistical analyses reported here were performed at the sensor level. For the electrical signal, the PO7 electrode located contralateral to the probe was selected. Magnetic sensors located contralateral to the probe with the maximum response at the time of interest were selected and averaged reversing the polarity of efflux-component of magnetic response as detailed in figure 3.4 in the methods section. Statistical analyses were hierarchically conducted as follows: first, a 2x2 repeated measures analysis of variance (ranova) using as main factors: stimuli presentation type (Onset vs. Continuous) and probe-conditions (match target vs. non-match target) were conducted. Whenever the ranova test was significant, pair-wise comparisons were performed between probe-conditions. A time-sample-by-time-sample sliding window approach was used. Mean amplitudes were taken over successive intervals (20ms, step size = 2 samples) and tested for significant differences between probe-conditions. A p-value < 0.05 was established as a criterion to reject the null hypothesis, and only when

five consecutive intervals reached statistically significant values were considered as significantly valid effects.

4.1.5 Neurophysiological results

Figure 4.2a,b and c show ERPs waveforms (PO7) elicited by probe-conditions as a function of stimuli presentation type (continuous and onset) of the attended color. Modulations of the negative (N1) responses were observed in both continuous and onset conditions according to probe-conditions: match target (solid black lines) and non-match target trials (black dash lines). Notably, the GCBA response to onset condition was larger (blue line) than in the continuous condition (pink line) as corroborated in the difference waveforms in figure 4.2c. A 2x2 ranova validated this effect with main factors *probe-conditions (*match and non-match) and *stimuli-presentation type* (continuous versus onset).

The ranova revealed a significant main effect of stimuli-presentation type (continuous versus onset) in the range between 45-123ms, 143-157ms, and 177ms-490ms. As well as the main effect of probe-condition (match versus non-match) was found between 150ms to 245ms and 302 to 471ms. Significant interaction effects between stimuli-presentation type and probe conditions appeared around 188ms-225ms and 357 to 397ms. Importantly, no significant interaction effect was observed between probe-conditions and stimuli-presentation type in the time range of the P1 component around ~100ms.

The MEG response reflects the efflux-influx collapsed waveforms from sensors located contralateral to probes (see Methods figure 3.4). Figure 4.2d and e show match minus non-match difference waveforms to each stimuli-presentation type. The upper panel displays the sensor response to the maxima magnetic field for the first modulation and the lower panel the sensors corresponding to the second magnetic response. The magnetic responses confirmed the presence of two modulations appearing roughly at ~200ms and ~260ms in both presentation conditions (continuous = pink lines; onset = blue lines). The first response appearing at ~200ms was smaller for the continuous condition relative to the onset condition. The opposite happened for the second neural GCBA response at ~ 260ms, where the response to continuous was larger than in onset condition (see figure 4.2e).

A 2x2 ranova with factors: probe-condition and stimuli-presentation type confirmed a main effect of probe-condition from 4-22msm, 155-281ms, and 326-500ms (upper; figure 4.2d) and from 170-202ms and 235-282ms for sensors describing the second modulation (lower; figure 4.2e). Similarly, a significant main effect of the stimuli-presentation type was found from 379-395ms and 457-500ms (upper, figure 4.2d) and 442-500ms (lower figure 4.2e). A significant interaction effect between the factor probe-condition [M vs. NM] and the stimuli-presentation type appeared at 186-202ms and~ 260 to 292ms (green shadow area figure 4.2d) and 216-257ms and 320-338ms (green shadow area figure 4.2e). These results, therefore, confirmed that the stimuli-presentation type in the focus of attention does not account for the very early GCBA modulation.

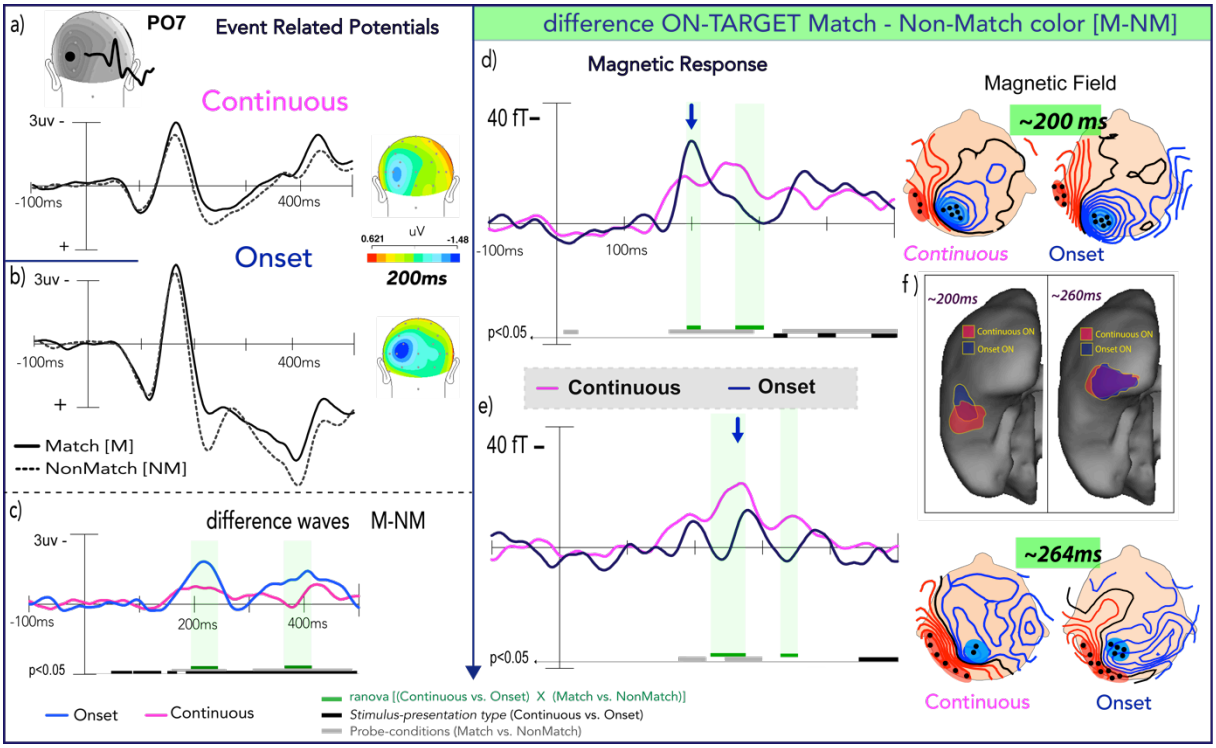

Figure 4.2a and b show ERPs waveforms from the PO7 electrode according to probe-conditions and type of stimulus presentation. Topographic maps of electrical response are illustrated for difference conditions: M-NM at 200ms. C shows the difference waveforms M-NM for continuous condition (lilac line) and onset (blue line). The green shadow areas indicate the timing when the ranova was significant. d) MEG difference waveforms M-NM for both stimuli-presentation types (continuous and onset) are plotted. Magnetic field distributions for the M-NM response to continuous and onset at two times of interest ~ 200ms and ~ 264-270ms and their corresponding current source densities.

By analyzing the magnetic field distribution together with the underlying current sources (see figure 4.2f), it is visible that in both continuous and onset conditions, the response at ~200ms is localized to more anterior regions of extrastriate visual cortex, while the second peak is localized toward more posterior regions.

In summary, the data suggest that the stimuli-presentation type in the focus of attention does influence the GCBA pattern. Contrary to our prediction, no GCBA effects were found in the P1 time range, neither in the onset nor the continuous condition. Those findings are in contrast to previous ERP studies (Moher et al., 2014; Zhang & Luck, 2009,) which reported such effects around ~100ms after stimulus onset. Our results are, however, consistent with the findings reported by Bartsch et al., (Bartsch et al., 2015, 2017) who demonstrated that the GCBA response typically appeared in a later time range around 160-300ms in the form of a sequence of two modulation phases in higher and lower level extrastriate visual areas. Those phases were shown to reflect separable cognitive operations ("template matching" and "discrimination matching") (see also Bondarenko et al., 2012).

An outstanding observation is that in the continuous condition, the first phase of the GCBA response (~190-200ms) shows a significantly smaller amplitude modulation than in the onset condition. This smaller initial response in the continuous condition is then followed by a larger late GCBA modulation reaching a maximum of around ~260-270ms relative to the onset condition. This attenuation of the first response in the continuous condition comes as a surprise, which warrants further clarification. Several possible mechanisms could be responsible for this outcome, but I will focus on the most likely

alternatives. One possibility is that mere low-level stimulation differences account for it, another possibility is that the actual probe-response indexes a distractor suppression processing, and the third possibility is that attenuation of the response indexes an attentional tuning mechanism.

4.1.5a Adaptation

It is possible that the continuous presentation of the attended color led to some color adaptation phenomenon. For example, when the target color was red, subjects viewed a color of the red range for some time before the actual target red was reached. It was not the case in the onset condition. Then, adaptation would attenuate the response to red accordingly. One way to address this possibility is to contrast the M-NM difference ON-TARGET with the match-probe condition when the probe appears off-target, i.e., when the attended circle and the probe share the same color, which is not the attended color (No-Attention) for continuous trials. This comparison is relevant to rule out the possibility that the data were explained by pure sensory adaptation in the visual system due to the continuous stimulation. If that were the case, adaptation should appear as well for color probes matching the target and the non-target color.

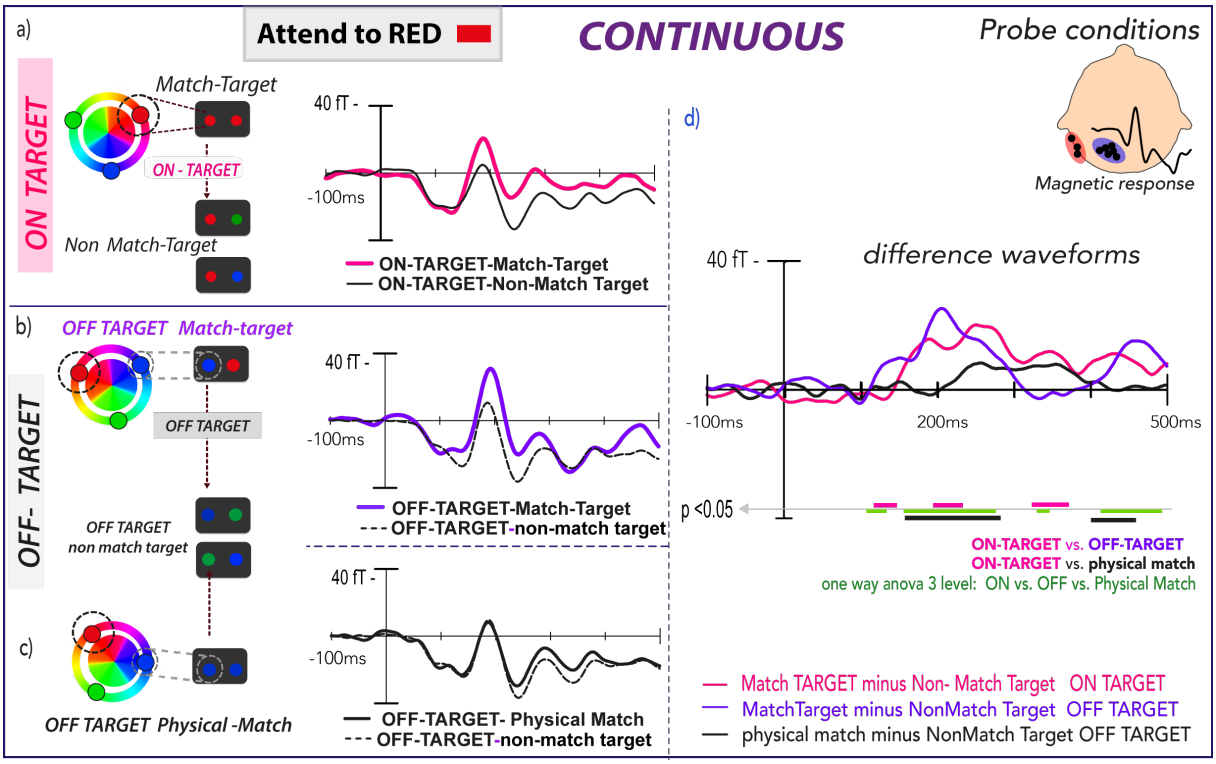

Figure 4.3. It illustrates three probe-conditions responses compared to continuous stimuli-presentation. In the right corner of the figure, it is shown the location of sensors used in the grand averaged waveforms. Sensors were located contralateral to the probe and selected based on the maximum response at ~ 200ms. The probe-conditions compared here are illustrated in a, b, and c. Red as the target is used here, but the same rule was applied for blue or green when target colors. D shows three difference waveforms [N-NM] comparing ON-TARGET N-NM, OFF-TARGET N-NM, and OFF-Target physical match. The colored lines below the waveforms mark the timing when the statistical analysis was significant ($p < 0.05$). GREEN: ranova one-way, three levels are comparing the three difference-responses. BLACK: pair-wise comparison between ON-TARGET versus OFF_TARGET physical match condition. PINK: pair-wise comparison between ON-TARGET_N-NM versus OFF-TARGET_N-M condition.

The OFF-TARGET physical match trials (attended circle and probe have the same non-target color; figure 4.3c) were compared with OFF-TARGET non-match trials (the attended circle and probe have different non-target color; figure 4.3b) for the continuous condition to compute the off-target difference.

As figure 4.3d shows, the OFF-TARGET physical match and non-match conditions were not different, ruling out that adaptation accounts for the attenuation of GCBA response. In contrast, consistent with the sensory bias for the attended color, when the latter is presented in the probe OFF-TARGET, a clear GCBA effect is visible (figure 4.3c, d; solid violet lines). The effect size of this response enhancement to the target color is notably bigger OFF-TARGET than ON-TARGET. This latter observation brings us to a further possibility more related to an attentional mechanism.

A one-way 3-level ranova comparing the three difference-waveforms (ON-TARGET M-NM, OFF-TARGET M-NM, and OFF-TARGET physical match-NM; figure 4.3 a,-b,-c, left side) was conducted. The Ranova was significant during 115-130ms, 157-271ms, 320-328ms, and 412-419ms, as shown in figure 4.3d.

4.1.5b Distractor Suppression

The target probe of the continuous condition is a more disrupting distractor because it contains a relevant color, potentially interfering with the current task in the focus of attention (Gaspelin & Luck, 2018). Thus, in the continuous condition, subjects may set themselves to more effectively attenuate the distracting influence of the matching probe in particular when approaching the target color. The present data do not allow ruling out this explanation.

4.1.5c Attentional Tuning

In the continuous condition, subjects view the attended stimuli continuously, allowing for a progressive increase of color selectivity when approaching the target color. Such color tuning at the neural population level appears due to a pruning (or response attenuation) of color units less selective to the target color. In other words, color tuning would reduce the number of units responding to the target color at the moment the color probe is presented (see the STM proposal; Tsotsos, 2011; Tsotsos et al., 1995) exactly as it was found in this experiment in the continuous condition.

The Selective Tuning model is a theoretical framework accounting for attentional selection from a computational perspective. The STM states that attentional selection (tuned-selection) sharpens the response to the attended features by a WTA process that prunes away all unwanted feature-values surrounding the target value (Tsotsos, 2011; Tsotsos et al., 1995).

No such attentional tuning effect would be expected to appear for the onset condition with the consequence that the same target color elicits a larger response relative to the continuous condition. It is because, in the onset condition, more but less selective units add to the population response.

Color selection via attentional tuning seems to be a very likely mechanism to explain the attenuation of the first GCBA response. STM's predictions for the color domain have been recently tested, particularly regarding the center-surround profile of color selectivity. This color selection profile has been shown using behavioral (Tombu & Tsotsos, 2008; Wang et al., 2015) and neurophysiological indices (Bartsch et al., 2017; Störmer & Alvarez, 2014).

4.1.6 Conclusions

Taken the data together show that both *stimuli-presentation type* onset and continuous elicit a sequence of two GCBA modulations with the first modulation arising from anterior extra-striate cortex and the later arising from more posterior regions in visual cortex (Bartsch et al., 2015, 2018, 2017; Bondarenko et al., 2012).

Pre-biasing the color information by being presented continuously in the focus of attention turns out to have differential influence on the phases of the GCBA response. The first GCBA modulation arising ~190-200ms was smaller in the continuous condition than in the onset trial-by-trial condition. The second modulation with a maximum peak around ~260-270ms was larger in the continuous than the onset condition.

Importantly, no evidence was found in support of the hypothesis that stimuli-presentation type accounts for the presence versus absence of a P1 modulation (~100ms) indexing GCBA seen in previous studies (Moher et al., 2014; Zhang & Luck, 2009). Critical experimental design differences could likely account for such discrepancy, including feature-priming effects, stimuli duration (offset effects of probes: 100ms vs. 300ms), luminance changes, level of difficulty, etc. For example, feature-priming effects might explain early differences regarding GCBA because in the two studies reporting a modulation of the P1 component (Moher et al., 2014; Zhang & Luck, 2009) color assignments of target and distractor color were kept the same for half of the blocks or the whole experiment.

The sequence of two GCBA modulations appearing at ~200ms and ~ 260ms in both continuous and onset conditions are in line with previous studies suggesting that GCBA modulates the N1 and N2 waves (feedback signals) indexing cognitive processes of "template matching" and "discrimination matching, "respectively. Notably, the amplitude of the N1 wave was highly modulated as a function of stimuli-presentation type in the focus of attention so that in the continuous condition, it was substantially attenuated relative to the onset condition.

Although differences in the pattern of response between continuous and onset conditions in the GCBA effects are well explained by Selective Tuning, alternative interpretations will be discussed in the discussion section.

4.2 Experiment 2

As described before, whenever there is a many-to-one convergence of neural signals, selective attention serves to reduce the interference from the irrelevant information and increase the signal-to-noise ratio of relevant stimuli neural signals (Desimone & Duncan, 1995; Tsotsos, 2011; Tsotsos et al., 1995). According to the STM, attentional selection sharpens (tunes) the response to the attended features by a top-down WTA process where all unwanted features responses are pruned away in the visual hierarchy.

From experiment one, it was known that presenting the continuous stream of colors (distractors) approaching the attended color presets a bias to the target color allowing the system to pre-tune into the target color.

Whether selective tuning mechanisms could operate when no pre-bias of the attended color is allowed (onset trial-by-trial presentation), but color selection requires high resolution is something that has not been tested yet.

Experimental data have shown that feature-based attentional tuning has its most significant effect when relevant features are embedded in feature noise (Ling, Liu, & Carrasco, 2009). It is believed so because the target feature selection profits most from the inhibition of neural units tuned to non-attended features (Tsotsos et al., 1995). In the domain of color selection, a tuning response is expected when distractor colors are similar to the target color. These effects might occur because color selection requires higher color resolution to discriminate the target from a very similar distractor color by discarding the neural signals not tuned to the target.

Here, target-distractor (T-D) color similarity in the focus of attention varied in two levels and evaluated how the GFBA response is modulated. If the global response of color selection were increased by inhibiting the non-attended feature signals, the probe-response would be smaller when T-D color similarity increases relative to less similar T-D colors condition.

The response to probes matching versus non-matching the target color (M-NM) was compared for two levels of T-D color similarity for testing the previously stated hypothesis. T-D color similarity is referred to as the color distance between the target and distractor (T-D) in color space, i.e., the angular distance in circular color space between the target color and distractor color-value within the same hue category (see figure 4.5).

In the first step, the color distance between the target and distractors was set. Three cardinal colors were used as targets and ten corresponding colors as a distractor for each target (angular distance within the HVS color wheel). Then, based on the individual performance range from task 1, two sufficiently different color distance values were selected. In the low-T-D color similarity condition, the distractor color was the color that yielded task-accuracy above 90%. In comparison, in the high-T-D color similarity condition, the distractor color was the color that yielded task-accuracy of 65-90%. The color similarity values were individually adjusted so that they were comparable across subjects.

In the second part of the experiment, the GCBA neural indices were compared as a function of the level of T-D color similarity (low vs. high) in the focus of attention.

4.2. Experiment 2 Section A

Here, behavioral indices such as response accuracy (%), the response time (ms), and sensitivity (d') are analyzed as a function of target-distractor similarity (10 color distances). The analysis was conducted separately for each target color (red, blue, and magenta) with their respective distractor colors (red-to-orange, blue-to-violet, and magenta-to-red).

4.2.A-1 Subjects

Twenty-four (mean age= 27.7, SD =4.4, range = 21-34 years old) participants took part in the experiment. One participant was left-handed, and 13 from total were women.

4.2.A-2 Stimuli

Stimuli consisted of two circles displayed in the lower quadrant of the visual fields on a grey background. The circle on the left visual field was the attended circle, and it was divided into two halves containing the target color and distractor color on each side.

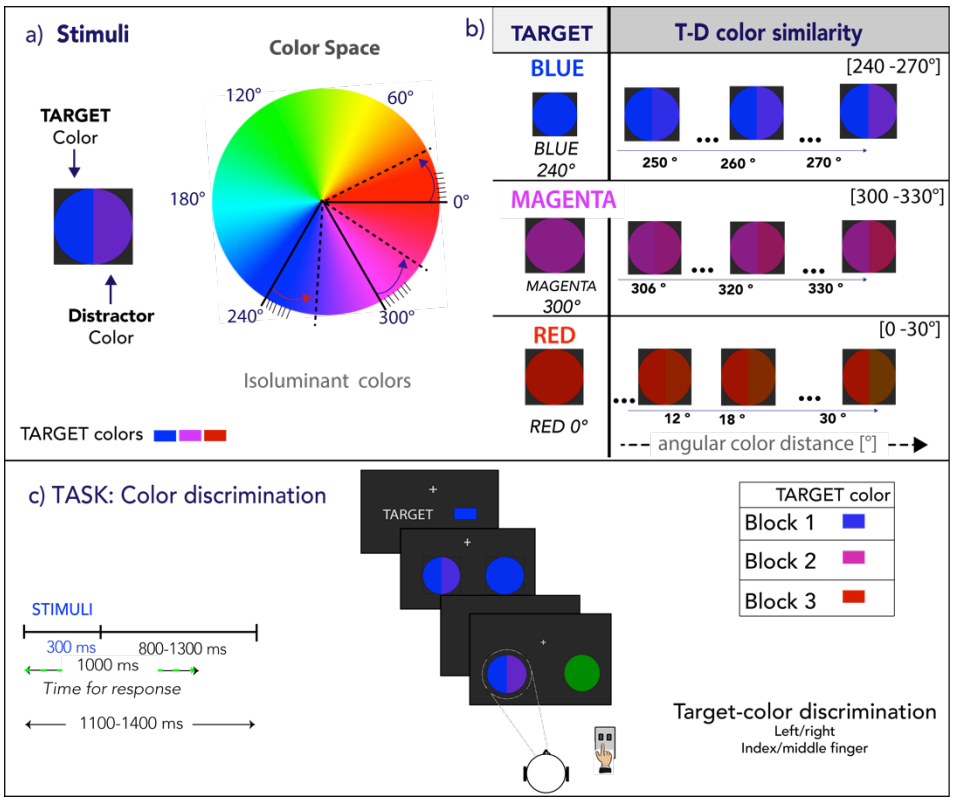

Figure 4.5. a) Schematic illustration of stimuli used in the experiment. Stimuli consisted of circles divided into two halves colored with one target color (red, blue, and magenta) and one out of ten respective distractor colors. The smaller the angle values were, the more similar target and distractors were. Target and distractor colors appeared 50% in the left and 50% of trials on the right side of the attended circle in random order. b) Task and temporal structure of trials. Subjects' task consisted of indicating whether the target color was on the left or right side of the target circle by pressing one or another button using their index or middle finger.

The target color was presented on the right side of the attended circle in 50% of the trials, while it was on the left side in the other 50%. The circle displayed in the right visual field (probe) was task-irrelevant and uni-colored with the current target color or with another color (gray, yellow, or green). All colors used in this experiment had the same saturation value. Hue-values were determined by dividing the HSV color wheel into 180° (360°) equidistant units (angular distance) in the same luminance *niveau* (35 cd/m^2) see figure 2.1.

Table 1. RGB values, luminance, and target-distractor values used in experiment 3.

RED	Angular position (°)	RGB			Luminance	BLUE Angular position (°)	Angular position (°)	RGB			Luminance	MAGENTA	Angular position (°)	RGB			Luminance
TARGET	0	160	0	0		TARGET	240	0	0	242		TARGET	300	136	0	136	
	2	160	5	0			242	8	0	243			302	137	0	132	
	4	160	11	0			244	16	0	242		d1	304	139	0	129	
d1	6	160	16	0			246	24	0	241		d2	306	140	0	126	
d2	8	159	21	0			248	32	0	239		d3	308	141	0	122	
d3	10	156	26	0		d1	250	39	0	236		d4	310	142	0	119	
d4	12	151	30	0		d2	252	47	0	234		d5	312	143	0	115	
d5	14	146	34	0		d3	254	54	0	232		d6	314	144	0	111	
d6	16	141	38	0		d4	256	61	0	229		d7	316	145	0	107	
d7	18	136	41	0		d5	258	68	0	226		d8	318	146	0	102	
d8	20	133	44	0		d6	260	75	0	224		d9	320	147	0	98	
d9	22	129	47	0		d7	262	81	0	220		d10	322	148	0	94	
d10	24	124	50	0		d8	264	86	0	214			324	149	0	89	
	26	120	52	0		d9	266	91	0	211			326	150	0	85	
	28	115	54	0		d10	268	96	0	205			328	151	0	81	
	30	111	55	0			270	100	0	200			330	152	0	76	
COLOR		RGB															
Yellow	60	68	68	0		Gray-background		65	65	65							
Green	120	0	73	0													
Cyan	180	0	71	71													

35 cd/m^2 | 35 cd/m^2 | 35 cd/m^2

Three target colors were used: red, blue, and magenta and 30 distractor colors, 10 for each target color in that way that distractor colors differed from target but varied within the same hue-category. Distractor colors varied from the target within a range of 2- 30 degrees (angular degrees):

$$2° > \text{T-D color distance} > 30°$$

The T-D color similarity took ten values going from very close-to-further away from the target. Target-blue was fixed at 240°, and blue-distractors were within the range of 242°-270°. Target-Red was fixed at 0°, and red-distractors varied from 2° to 30°. Target-magenta was fixed at 300°, and magenta-distractors varied from 0° to 330°. Table 1 describes the actual color values used for the three targets and their corresponding distractors.

4.2.A-3 Task and procedure

Subjects performed a color discrimination task divided into three blocks, one block for each target color (blue, magenta, and red). Every block started with a frame lasting 2000ms to instruct subjects about the target color. The target and probe circles were displayed on a grey background for 300ms, followed by an Inter-stimulus interval (ISI) of 800-1300ms (uniform distribution). Subjects were seated at a 1-meter distance from the screen, and they were asked to fixate a central fixation cross while covertly attending to the left visual field. The subjects' task consisted of indicating whether the target color was on the left or right side of the attended circle. The probe displayed in the right visual field was irrelevant for the task. Subjects used their index and middle finger to indicate their response (Figure 4.5b).

4.2.A-4 Results

The mean and standard deviation of correct responses and response time were calculated separately for each target color as a function of T-D color similarity. One-way repeated-measures analyses of variance (10-level ranova) on accuracy and response time were conducted independently for each target color.

Figures 4.6a and 4.6d show accuracy and response time, respectively, when the target was blue. Overall, responses were less accurate $F(9, 207) = 40.51$, $p < 0.001$, and slower $F(9, 207) = 4.50$, $p < 0.001$ on trials where the target and the distractor were more similar in comparison to trials where the color similarity was lower. A similar pattern was observed for red (see figure 4.6b and 4.6e). Responses were less accurate $F(9, 189) = 57.70$, $p < 0.001$ and took more time $F(9, 189) = 24.02$, $p < 0.001$ the closer the target color was to the distractor colors. In figure 4.6c and 4.6f, the response to target-magenta is shown. Again, the larger the target-distractor similarity, the less accurate ($F(9, 144) = 9.25$, $p < 0.001$) and slower ($F(9, 144) = 20.70$, $p < 0.001$) the responses were. A signal detection analysis for each target color revealed an overall increment in sensitivity (d') as a function of target-distractor color similarity in all target colors. Figure 4.6g plots the sensitivity in the y-axis and the target-distractor similarity the level in x-axis for each target color.

Sensitivity (d') was computed using the *z score* of hits and false alarms. When subjects did not have false alarms or miss in 1-to-3 color-distance, data-points were adjusted as follows: 1/(2N) and 1- (1/(2N) for false alarms and hits respectively (Macmillan & Creelman, 2005). However, when subjects did not have false alarms or miss in more than three color distances, data from those subjects were excluded from SDT analysis.

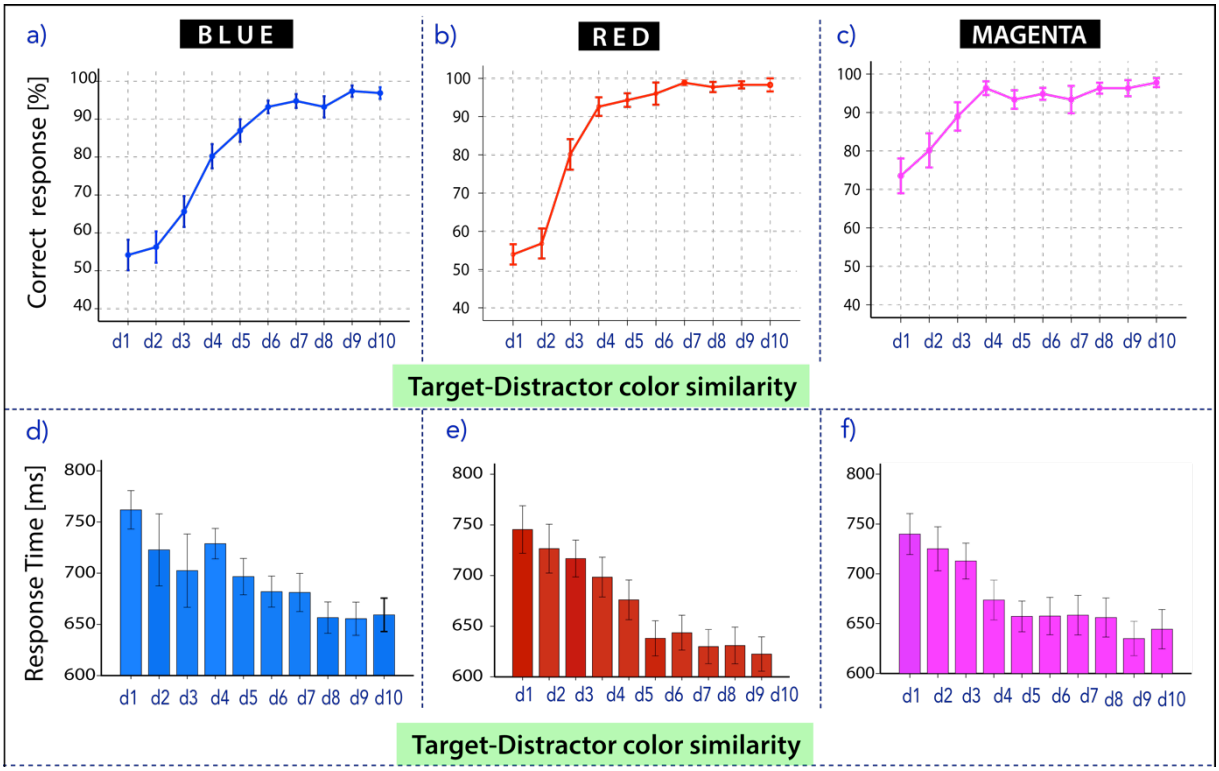

Figure 4.6a, b, and c show the mean and standard errors of accuracy (percentage of correct response) as a function of target-distractor color similarity. In d, e and f bars-graphs show means and standard errors of response time (RT) as a function of target-distractor color similarity. G shows three dot-plots of sensitivity against target-distractor similarity for each target color. Each data- point represents the mean across subjects. H illustrates sensitivity as the difference between means of signal-distribution (target) and noise distribution (distractors). Error bars are + 1 s.e.m

4.2.A.5. Conclusions

In summary, the data confirm that response accuracy, response time, and sensitivity followed a gradual increment as a function of the color distance between the target and the distractor.

4.2.Experiment 2 Section B

The second part of this experiment asked whether color selection involves selective tuning (Tsotsos et al., 1995) when T-D color similarity in the focus of attention increases and stimuli are presented in an onset trial-by-trial manner.

In experiment one, we showed that the early GCBA response (~200ms) was attenuated when the continuous stream of colors (distractors) approached the attended color, but not when the color

stream was approaching a non-attended color. These findings raise the question of whether similar tuning mechanisms would operate for highly similar target and distractor colors when pre-tuning into the attended color is not possible because the stimuli are presented in an onset trial-by-trial manner.

Verifying that color selection involves selective tuning is not trivial. Given that it makes qualitative predictions about amplitude modulations of the ERP and ERMF response, some hypotheses could be established. Figure 4.7 shows a graphical description of the potential neural operations underlying color selectivity. Figure 4.7a illustrates the response of the neuron tuned to the target color (red) when no attention process is involved. Figure 4.7b and figure 4.7c describe two alternative mechanisms underlying color selectivity: gain enhancement and selective tuning by surround attenuation. Figure 4.7b illustrates the surrounding attenuation (SA) profile of the neurons' response less tuned to the target; such SA is compatible with the selective tuning mechanism. Figure 4.7c shows a gain enhancement of the neurons' response tuned to the target.

Thus, verifying that color selection involves selective tuning when fine color discrimination is required can be tested as follows:

If color selection involves a selective tuning mechanism pruning away the unwanted signals, the early GCBA response (~200ms) would be smaller for high T-D similarity relative to the GCBA response when T-D similarity is small in the focus of attention (see figure 4.7b).

Alternatively, if color selection would not involve selective tuning, a similarly sized GCBA response (~200ms) would be expected for high and low T-D similarity.

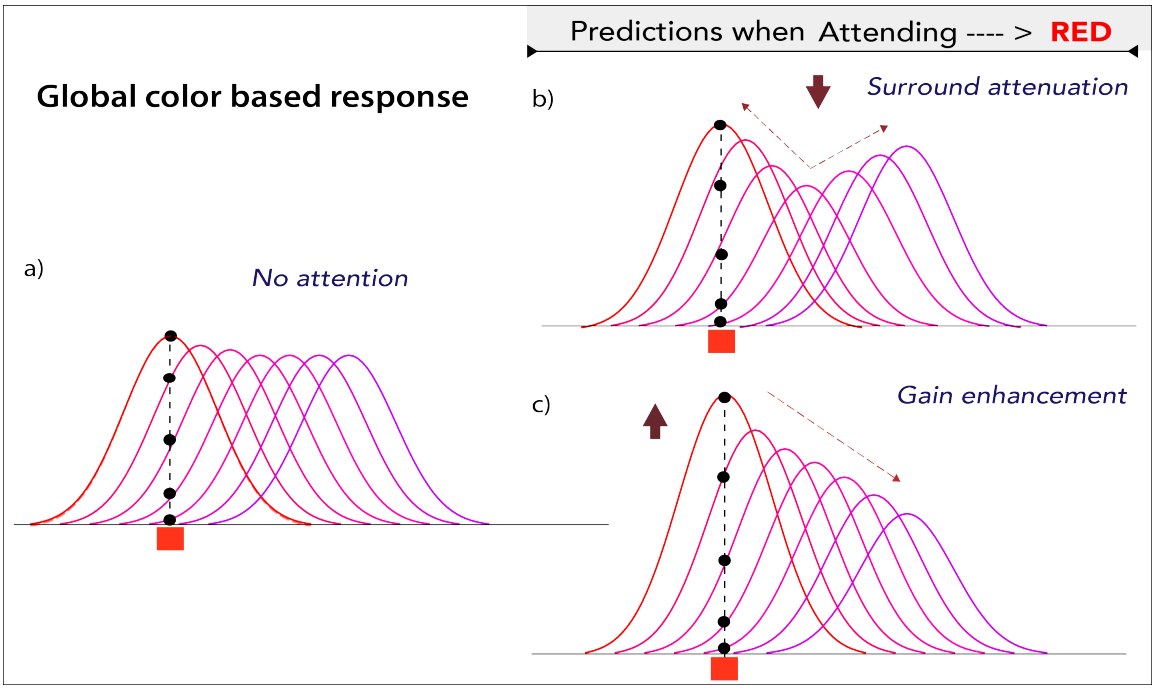

Figure 4.7 illustrates the expected global-color based response to high Target-Distractor similarity. A shows the hypothetical response when no attention is involved. B illustrates the hypothetical response when selective tuning is the underlying mechanism behind color selectivity. C illustrates the hypothetical response when gain enhancement is the underlying mechanism.

4.2.B.1 Subjects

The same twenty-four participants from section A took part in section B of experiment 2.

4.2.B.2 Stimuli

Every trial consisted of two-colored circles, which were displayed each one in the lower quadrant of each visual field on a grey background.

Attended stimuli. As in the previous behavioral task, the circle on the left visual field was the attended stimulus; it contained the target color on one side and the distractor color on the other side. There were two distractor color-values selected based on the individual performance level reached in the previous task (section a). The two T-D color distances were used as an index of color similarity level (Low vs. High), as seen in figure 4.8a.

The T-D distance was determined for each subject individually; when necessary, it was adjusted online over the experiment to guarantee a roughly constant performance level range across experimental blocks. Figure 4.8b shows the average target-distractor color distance across subjects and blocks. The difference between high- and low- T-D similarity conditions for each target color was statistically validated: blue $t(23) = 50.72$, ($p < 0.001$), red $t(23) = 42.77$, ($p < 0.001$), and magenta $t(23) = 48.64$, ($p < 0.001$) (figure 4.8b).

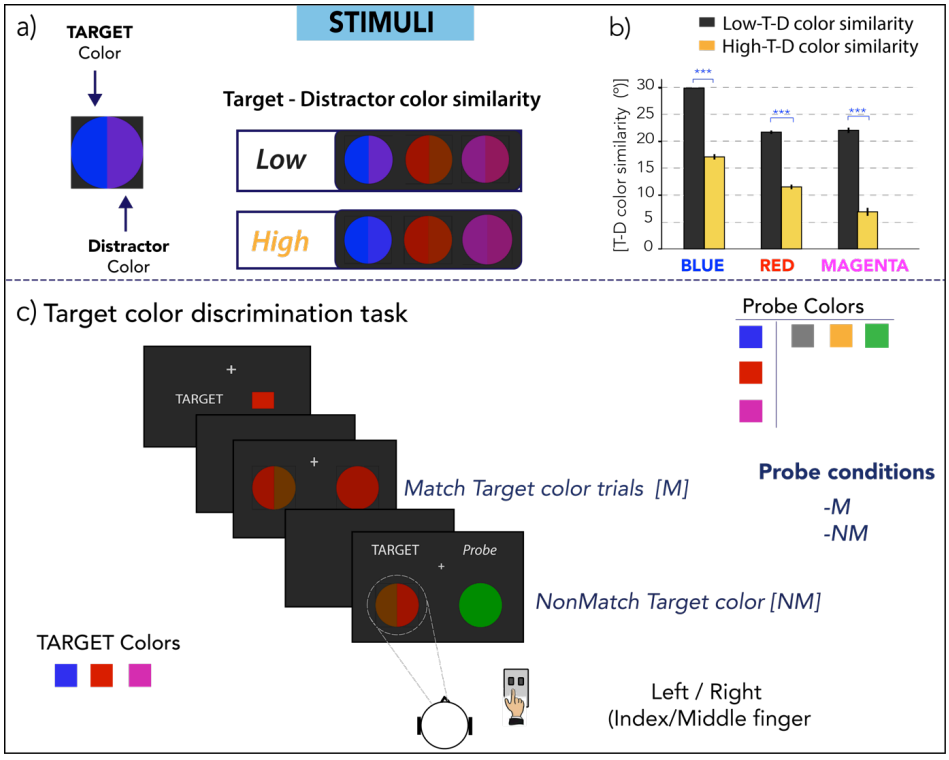

Figure 4.8a illustrates the stimuli used in the experiment. Target colors were red, blue, and magenta and two distractor colors for each target. b) The bar graph shows the average across subjects of target-distractor color distance for low and high T-D similarity in the focus of attention for each target color. Error bars are ± 1 s.e.m. *** p-value < .001 c) Task and type of trials are illustrated, stimuli are scaled in size. Printed labels such as "TARGET" and "probe" were not presented in the task, only at the beginning to indicate which color subjects had to attend. Subjects indicated their response by pressing one or another button using their index or middle finger.

Unattended Stimuli. The circle placed on the right visual field was the *probe*. It was uni-colored either with the current target color or another non-target color (equally and randomly presented as the target). The probe was a task-irrelevant stimulus.

Trials were blocked by target color and T-D similarity (High vs. Low) in the focus of attention. Thus, we had blocks of red low-T-D similarity, red high T-D similarity, blue low-T-D similarity, blue high T-D similarity, magenta low-T-D similarity, and magenta high T-D similarity trials. Each block was repeated two times, amounting to a total of 12 blocks of 152 trials each. Each block lasted approximately 5 minutes and included five small pauses for blinking. The order of blocks was interleaved between colors and counterbalanced across subjects in a way that one group of subjects began with red, another with blue and another with magenta low-T-D similarity and high-T-D color similarity blocks respectively. Each block was repeated two times using the same order of colors in the second round of blocks for each subject.

Each block started with a frame instructing subjects about the target color and the difficulty of the task. Every trial consisted of two circles displayed in a grey background for 300ms followed by an Inter-stimuli interval (ISI) of 800-1300ms (uniform distribution) (figure 4.8c-d).

4.2.B.3 Task

Subjects performed a target color discrimination task: they had to indicate whether the target color was on the left or right side of the attended circle by pressing one or another button: index finger (left-side) and middle finger (right-side).

4.2.B.4 Data analysis

EEG and MEG signals were epoched using 200ms as baseline and 700ms following the stimuli onset. Epochs with recording, motion artifacts, eye blinks and eye movements were excluded using a peak-to-peak threshold criterion for MEG (M= 3.35 fT, SD=0.32fT, range= 3 -3.9fT) and EEG signal (M=116uv, SD= 8.6uv, range= 110 - 130uv). Grand averages were calculated only in trials with correct response according to four probe-conditions: Low-T-D color similarity Match target color [M], Low-T-D color similarity Non-Match target color [NM], High-T-D color similarity Match target color [M] and High-T-D color similarity Non-Match target color [NM].

Brain signals were analyzed using a 2x2 ranova design comparing the response to Match versus Non-Match target color trials as a function of T-D color similarity (Low vs. High).

4.2.B.5 Behavioral Results

Mean and standard errors of accuracy and response time were calculated according to probe-conditions and T-D similarity. Statistical analyses compared behavioral indices using a 2x2 ranova with the factors: probe-condition (Match versus Non-Match) and T-D similarity (Low vs. High). As expected, response accuracy was higher in the low- T-D similarity (M=96.85) than in the high- T-D similarity condition (M=84.48), $F(1, 23) = 193.31$, $p < 0.001$. No significant main effect was found for probe-condition $F(1, 23) = 1.98$, $p = 0.173$, and there was no interaction effect between probe-condition and T-D similarity $F(1, 23) = 0.94$, $p = 0.35$ (see figure 4.9).

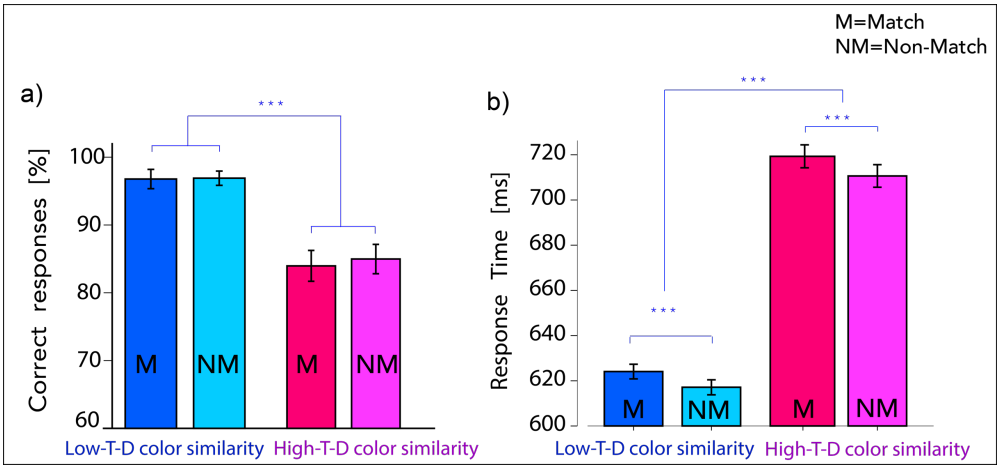

Figure 4.9 shows bars graphs for means of percentage of correct response (a) and response time in milliseconds in (b) according to T-D similarity (low versus high) and color conditions in the probe. M=Match color and NM=Non-match color. Error bars are ± 1 s.e.m. ***p-value < .001

An analogous 2x2 ranova for response time revealed an interaction effect for T-D color similarity and probe-condition F (1, 23) =8.90, p = 0.007; and significant main effects of T-D color similarity F (1, 23) = 1967.70, p < 0.001 and probe-condition F (1, 23)=1100.51, p <0.001. Responses to non-match trials were faster than match trials in both T-D similarity levels (low: Match = M=624.09; Non-Match= M=617.12; High: Match M=719.33; Non-Match: M=710.65) (figure 4.9).

4.2.B.6 Neurophysiological data

GCBA effects were computed by comparing the brain responses to probe-conditions when the probe matched versus when it did not match the target color (Match=M versus non-match= NM trials). First, we compared the electrical response at the PO7 electrode located contralateral to the probe. Figure 4.10a and 4.10b show the waveforms for Match and Non-match trials for both levels of T-D similarity: low (black lines) and high (lilac lines). A 2x2 ranova analysis with probe-conditions: M versus NM and T-D similarity: high and low revealed a main effect of T-D similarity at 72-82ms and 208-473ms. A significant effect of probe-condition during 54-64ms, 98-125ms, 155-235ms, 369-398ms, 432-469ms, was observed and significant interaction effects between probe-condition and T-D similarity in time ranges 249-302ms, 404-459ms, and 469-500ms were also found.

Regarding the magnetic response, figure 4.10c and 4.10e show the GCBA responses at selected sensors sites showing the maximum field response contralateral to the probe. Topographical maps of the magnetic field distributions show the difference response M-NM according to T-D similarity (low and high) roughly at ~200 and 300ms (see figure 4.10c and 4.10e). The black dots marked in the magnetic field distribution correspond with the location of the sensors selected.

The GCBA responses corresponding with low- T-D similarity (black lines) and high- T-D similarity trials (lilac lines) are overlaid. The GCBA response to low T-D similarity trials was larger than the response to high T-D similarity trials within the time window of 205 to 225ms and 253-318ms (significant interaction effect between probe-condition (M and NM) and T-D similarity (Low- and High). In the lower panel of figure 4.10e, the GCBA response for the second modulation phase shows that the low- T-D color similarity condition elicited a larger response than the high T-D similarity condition. The interaction

effect between probe-conditions and T-D similarity (M vs. NM and Low- vs. High- T-D similarity) was significant during the time range of 254-to 329ms, 344-372ms, and 449-500ms.

The main effect of T-D similarity from 238-325ms and a significant main effect of probe-condition during 54-64ms, 98-125ms, 155-235ms, 369-398ms, and 432-469ms were found for sensors in the upper panel. The 2X2 ranova revealed a main effect of T-D similarity (low-high) at 242-286ms and 309-346ms, and a significant main effect of probe-condition during 93-142ms, 199-210ms and 376-413ms for sensors in figure 4.10e (lower panel).

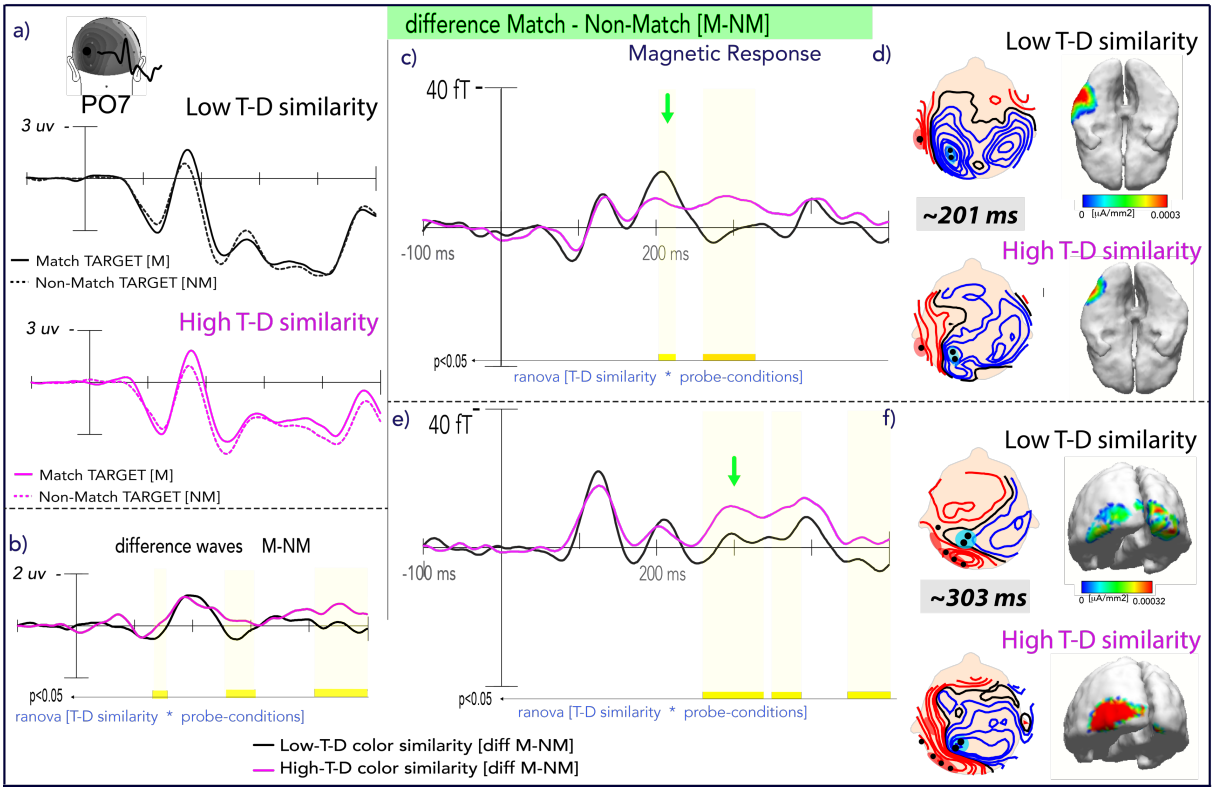

Figure 4.10a-b show the electrical response to probe-color (Match vs. non-match target) according to T-D color similarity in the focus of attention low- (black lines; a) and high (lilac lines; c shows the difference responses (M-NM) of low- and high T-D color similarity. Section d-e shows the waveforms of the magnetic response for the early GCBA modulation accompanied by their respective magnetic fields. Significant interaction effects between T-D color similarity (low and high) and probe conditions (Match and Non-match) are highlighted in the lower part of the waveforms with a yellow bar.

Current source density distributions were computed for the M-NM difference of both T-D color similarity levels (Low and High). The early GCBA modulation, which reached a maximum peak around ~200-228ms, was localized at anterior areas of the extrastriate visual cortex (figure 4.10d). The late response, beginning after ~250ms and reaching a maximum around ~303ms for high- T-D similarity, was more posteriorly located in the visual cortex (figure 4.10f).

4.2.B.7 *Conclusions*

In summary, our data confirm our main prediction that the GCBA response pattern varies depending on the T-D similarity in the focus of attention. The early GCBA response (~200ms) was smaller for high T-D similarity relative to low- T-D similarity consistent with the selective tuning account (see figure 4.7).

The attenuation of the early GCBA response indicates that color selection was likely resolved by selective tuning, i.e., a pruning of units the neural signal responding to non-attended features.

The late GCBA modulation (> ~260ms) was larger for high T-D similarity compared to the low T-D similarity level as expected. The amplitude increment of the second response presumably reflects a more selective response once the neural signals to unwanted features have been suppressed. A larger response to harder discrimination is consistent with previous studies where the response is typically larger when the task demands are higher in a more difficult task (Bartsch et al., 2018; Boudreau, Williford, & Maunsell, 2006; Garcia-Lazaro et al., 2018; Spitzer, Desimone, & Moran, 1988), (See results from experiment 3 of this work for GCBA response in particular).

The results of experiment 2, therefore, dovetail with those of experiment 1, where a similar early attenuation of the GFBA response was observed when the attended color stream approached the target color (continuous condition). The situation is comparable here, with high T-D similarity in the focus of attention requiring higher color resolution to differentiate the target from the distractor color. The STM proposes that tuning the coding the target feature to higher resolution is accomplished by a suppression of the response of units less optimally tuned to the target feature. Tuning, therefore, leads to a net attenuation of the ERP/ERMF response, because a reduced number of selective color units contribute to the population response.

Empirical data obtained in recent years using behavioral (Tombu & Tsotsos, 2008; Wang et al., 2015) and electrophysiological indices (Bartsch et al., 2017; Störmer & Alvarez, 2014) have supported predictions of the STM concerning the predicted center-surround profile of color selection. The closest to the present design is the work by Bartsch and coworkers, where a small attenuation of the response for probes with colors more similar to the target was observed during the late GCBA modulation (~275-390ms). At first glance, our data differ from Bartsch et al. (2017) concerning the time-range the attenuation was observed. However, it is likely that in Bartsch et al., (2017), no selective tuning appeared in the early GCBA phase (template matching phase), because the top-down definition of the target color did not require a high-resolution template at first instance. The task in Bartsch et al. (2017) consisted of discriminating the target color from a very different distractor color (red from green) in the focus of attention. In our experiment, the discrimination required higher color resolution, because the target was very similar to the distractor; hence, the much earlier onset of attentional tuning effects.

Data from this experiment allow us to rule out the possibility that the attenuation of the GCBA response could be explained by a suppression of the probe (Gaspelin & Luck, 2018), as discussed in experiment one. It was considered as an alternative interpretation because the target probe in the continuous condition might be a more disrupting distractor than in the onset task, because of the higher color selectivity required for the continuous task. Here, the experimental design allowed comparing the GCBA response between two conditions (T-D color similarity) where the stimulus presentation mode was the same (onset trial-by-trial). The attenuation of the response seen in the high-T-D similarity condition speaks against the possibility that attenuation of the GCBA reflects distractor suppression.

Another alternative worth discussing is that the response attenuation is only relative to an enhancement of neighboring colors. A couple of studies have shown that for small but not large T-D distances, the attentional gain enhancement to discriminate the target feature-value is shifted away from the target to neighboring feature-values. Here the response modulation due to the target and distractor show a larger difference (Hol & Treue, 2001; Scolari, Byers, & Serences, 2012). Thus, probing the target in the small T-D distance condition could result in a smaller response relative to the larger

color distance. It is not entirely possible to rule out this alternative based on our data. However, this possibility is unlikely as it implies that the control colors would be among the colors showing an off-target enhancement. Nonetheless, off-target enhancement may play a role in hard discriminations, which is worth to address further. It would require testing the neural response for gradually increasing T-D color distances (see Feature Research for a possible experimental design).

Part 2: Neuromagnetic indices of global attention- and reward-related selection in the human visual cortex.

In the second part of this work, we focus on the global reward-based selection (GRBS) and its relationship to GFBA. Although attention and reward are distinct concepts, in many neurophysiological experiments, they might be intermixed or confounded. Maunsell (2004) highlighted this issue in his seminal paper by pointing out that the increment of the firing response associated with attention could reflect the effects of reward, given that in almost all attention studies in the monkey, attention is typically motivated by reward. Thus, whether attention- and reward selection processes modulate the activity independently in visual cortical areas (Arsenault, Nelissen, Jarraya, & Vanduffel, 2013b; Hopf et al., 2015; Serences et al., 2010; Weil et al., 2010) or whether both reflect the same modulatory influence (Chelazzi et al., 2013; Della Libera & Chelazzi, 2009; Della Libera et al., 2011; Kristjánsson et al., 2010; Rombouts et al., 2015; Seitz et al., 2009; Serences, 2008) is something still in debate.

4.3 Experiment 3

The experiment three focuses on the dissociation of global task-related (GCBA) and reward-related (GRBS) modulatory effects in visual cortices. From a previous study (Hopf et al., 2015), it is known that attention and reward elicit similar global responses in visual regions (in terms of response amplitude and time-courses). Interestingly these responses seem to have an additive relationship (Hopf et al., 2015) compatible with the possibility that both are dissociable from each other to a certain extent. One way to test this idea, with the unattended probe paradigm, is to compare the probe response under varying attention demands on target selection (task difficulty) while keeping constant the reward-defining settings. Thus, using the experimental setup of Hopf et al., (2015) allows testing the probes responses (unattended stimuli) when matching the target color (T), the reward-related color (R), both target and reward (TR) or a control color (C).

Experimental manipulation of attentional load requires establishing task difficulty levels. In the first section of experiment three (3A), the rotation angle of the intersection between the target and the distractor color in the attended stimuli (3D sphere) was gradually varied to test whether it leads to variations in the task difficulty level (see figure 4.11b). The task consists of indicating whether the rotated angle of the target color is concave or convex oriented. Smaller rotation angle values correspond with higher task difficulty.

Based on individual task performance, two levels of task difficulty (easy and hard) were determined in the first behavioral experiment. The easy level corresponds to the rotation angle yielding to task-accuracy-response above 85%, while the hard condition corresponds to the rotation angle yielding a task-accuracy from 65 to 85%. In the second part of the experiment (section B), the GCBA and the GRBS responses were compared as a function of difficulty (easy and hard level). At the same time, reward settings were kept the same in both task-difficulty conditions.

4.3 Experiment 3 Section A

4.3.A-1Subjects

In this experiment eighteen participants took part (mean age= 26.72 ± 2.92, range 22 to 31 years old). All gave their informed and written consent and were paid for their participation (6 € /h). Eight were women, and all participants were right-handed and had a normal or corrected-to-normal vision. Data sets from two subjects were not included in the analysis reported in the first section (A) because those participants performed the behavioral task using different range orientation values. Nevertheless, all eighteen participants performed the main experiment when recording brain responses, and data from all of them are reported in section B.

4.3.A-2 Stimuli

Each trial consisted of two bicolored 3D spheres (diameter of 1.58° of visual angle), one placed in the left and one in the right visual hemifield, 1.6° below, and 2.8° lateral from fixation. The spheres were placed on a grey background (lum=10.6 cd/m^2). The attended stimulus was always located in the left visual field, while the probe (task-irrelevant color probe) was located in the right visual field. The attended sphere was divided into two halves, with each side being colored with one out of 5 colors: red, green, blue, yellow, and grey. The attended sphere was rotated in the plane to the left or right such that the contact line between the target and the distractor color projected as concave or convex edge onto the screen. The amount of in plane rotation varied among eight angular values from 0.5° to 4° in steps of 0.5° in both directions (concave and convex, 16 rotation angles in total, see figure 4.11). When determining the individual level of discrimination difficulty (behavioral experiment), only one color was used as a target (red), and the remaining colors were control colors presented randomly. This task consisted of a total of 320 trials, and there was no reward schedule.

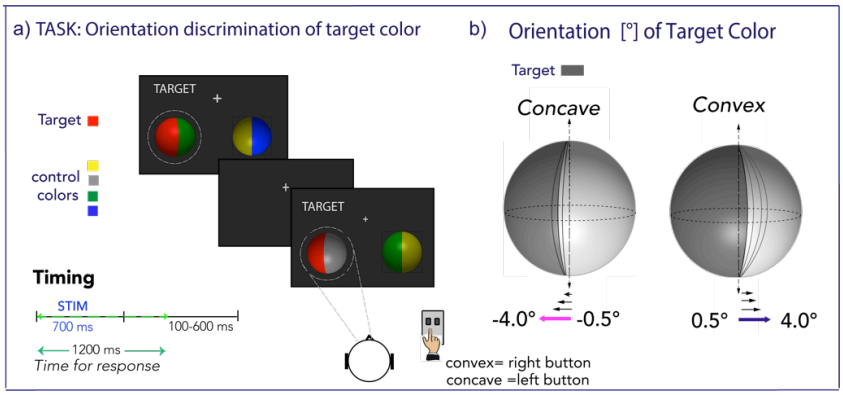

Figure 4.11 a) Colored 3D spheres were used as stimuli. Subjects task consisted of discriminating target color orientation (convex vs. concave) while varying the orientation values. b) Example of orientation-values used on the task sampling from -4° (convexity) to +4.0 (concavity) in steps of 0.5°.

4.3.A-3 Task and procedure

Each trial consisted of two spheres being displayed for 700ms, followed by a variable blank interstimulus interval (ISI) of 100-600ms (Uniform distribution). Subjects were instructed to fixate at the central fixation cross, while covertly pay attention to the attended stimulus in the left visual field and to ignore the color probe in the right visual field. The participants' task was to indicate whether the half-

sphere drawn in the target color was concave- or convex- by pressing one or an alternative button with the right index or middle finger.

4.3.A-4 Results (Behavioral experiment)

Mean and standard deviation of the task- accuracy (percentage [%] of correct responses) and response time (RT, ms) were calculated for each rotation value (0.5, 1.0, 1.5, 2.0, …, 4.0°). A one-way repeated-measures analysis of variance (8th level) using as main factor degrees of rotation (combined concave and convex) was separately conducted for accuracy and response time. Statistical analyses revealed that the accuracy level varied as a function of rotation angle $F(7,105) = 50.58$, $p < 0.001$. As expected, task-response was less accurate in smaller degrees of rotation angle than responses to larger rotation-values (figure 4.12a-b). Regarding response time, RTs varied as function of rotation angle $F(7,105) = 54.85$, $p < 0.001$. Overall the response to smaller rotation angles was slower than the response to larger rotation angles (figure 4.12c-d).

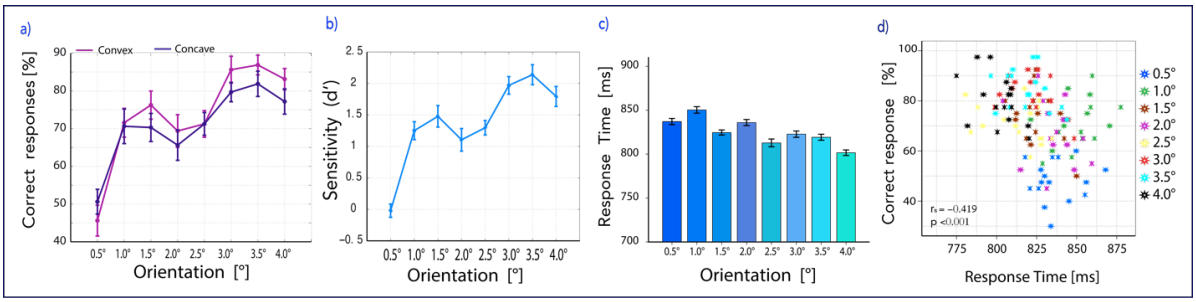

Figure 4.12a illustrates the response-accuracy as a function of orientation value sampling the range from 0.5 to 4° in both directions concave and convex b) Dots-plot shows sensitivity (d') as a function of orientation value; error bars are $\pm$ 1 s.e.m. c) Bars plot illustrates the response time in milliseconds for correct response trials according to orientation-values. D shows the correlation between response time and accuracy as a function of orientation.

4.3.A.5 Conclusions

The data show that behavioral indices: response-accuracy, response time, and sensitivity increased as a function of the rotation angle in the intersection between the target and distractor color in the attended stimulus. Two rotation angles leading to two sufficiently different task performance levels (easy and hard) were established.

4.3 Experiment 3 Section B

The second part of experiment 3 tests whether global color responses for task-related and reward-related bias vary as a function of task-difficulty (easy and hard). We hypothesize that if reward modulations were independent of task-related modulations (attention), then the response to target-probes would vary as a function of task-difficulty, but the reward-related response, instead, should not change. Alternatively, if reward and target modulations were linked, we would see the modulation of both target-probes and reward-probes response as a function of task difficulty.

4.3.B.1 Subjects

The same eighteen participants from section A took part in section B of experiment 3.

4.3.B.2 Stimuli

Stimuli were similar to the ones used in section A, with the difference that reward color definition was introduced here. On each block, one color was labeled as reward-related color signaling the probability of receiving a reward when this color appeared in the attended stimulus. Color assignments changed over the blocks, but they were similar for pairs of easy and hard blocks (figure 4.13b). All colors were used once as the target color and once rewarded color in easy and hard blocks. Trials were blocked by task-difficulty and target color; thus, there were in total ten blocks 5 for easy and 5 for hard condition each one corresponding to each target color. There were four color assignment orders (A, B, C, and D) distributed and counterbalanced across subjects to avoid primacy, recency, or priming effects to any particular color (see figure 4.13b showing order A as an example).

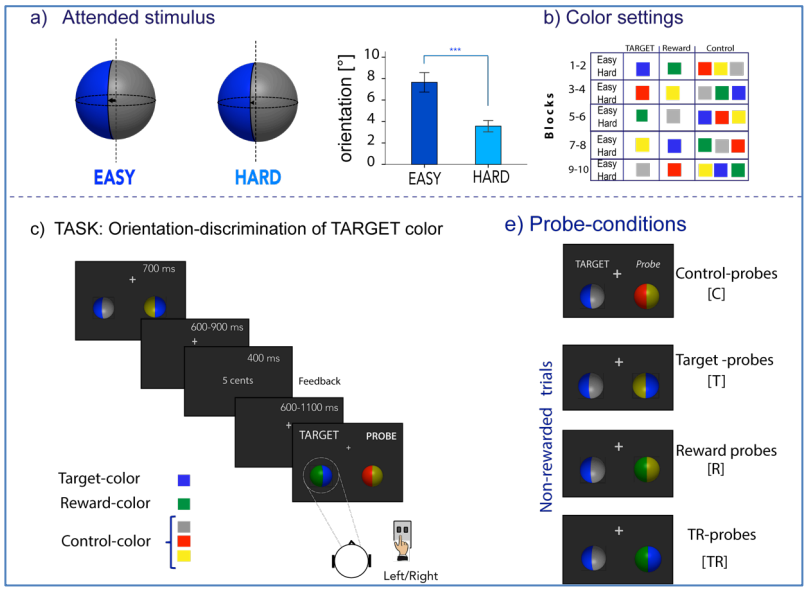

Figure 4.13 a) Schematic illustration of stimuli used in the experiment, the rotation angle of the target color (blue as an example) was set to two values leading to two conditions: easy and hard. The bar graph shows the average rotation-angle across blocks and subjects. Error bars are $\pm$ 1 s.e.m. *** p-value < .001 for t-test between easy vs. hard comparison. B shows color assignments for each pair of easy and hard blocks; here, order A is illustrated. c) Stimuli are scaled in size; see methods for a precise description. Printed labels such as "TARGET" and "PROBE" were not presented in the task. Subjects indicated their response by pressing one or another button using their index or middle finger. E shows the probe-conditions: control probes, target probes, reward-probes, and TR-probes.

Attended Stimulus: 3D sphere placed on the left visual field and containing the target color on one side and distractor color on the other side (left and right location within the sphere was equally frequent 50% left; 50% right). In 75% of total trials, the distractor color was a neutral color, and in 25% of the trials, the distractor was the reward color. The edge between the target and distractor color varied in rotation angle in both directions (concavity and convexity). Two rotation angles yielding to two different task-accuracy indices were selected (easy > 85%, and > 65% Hard < 85%). The task required indicating whether the target half-sphere in the attended location was concave or convex oriented. Task load increased with a decreasing rotation angle. Task-difficulty was adjusted to be equal as much as possible among subjects, and it was adjusted online during the MEG experiment to maintain constant the task performance rate across experimental blocks.

The rotation angles used for each subject were averaged across experimental blocks and statistically compared to validate that they were indeed different between easy and hard conditions (T= 9.84 df= 17, p<0.001; bar-plot in figure 4.13a).

Unattended stimuli (Probe): The probe was a task-irrelevant 3D sphere placed on the right visual field. The sphere was divided into two halves and colored with one out of four-color combinations. Control-probe (C): both sides were control colors, Target-probe (T): one side was colored with the Target and the other with a control color, Reward-probe (R): one side was colored with the Reward color and the other with a control color, and TR-probe (TR): one side was colored with the Target and the other with the Reward color. All probe-types had the same frequency of repetition, but the order of presentation was randomized over the block.

4.3.B.3 Task and Procedure

At the beginning of each block, subjects were informed about the target and reward color and difficulty of the task by presenting an instruction screen for 2000ms. Then each trail consisted of two spheres displayed on grey background for 700ms followed by an inter-stimulus interval (ISI) of 1300-1800ms (uniform distribution). On rewarded trials, there was an additional feedback-text frame presented for 400ms informing about the earned reward: "5 cents," or "0 cents," followed by an ISI of 600-900ms (uniform distribution).

Subjects were seated at 1m from the screen, and they were asked to fixate at the central fixation cross and covertly pay attention to the stimuli presented in the attended side (left visual field) while ignoring the probe. Subjects' task consisted of discriminating the orientation of the target by indicating whether the target color was concave or convex oriented. Subjects pressed one of two buttons (index=concave and the middle finger=convex). In total, participants performed ten blocks of 128 trials, each one lasting approximately six minutes each block. There were some small pauses within the blocks to allow blinking.

4.3.B.4 Reward-schedule.

The rewarded trials (25% of total trials) were those trials where the target and reward-related colors were presented together in the attended sphere. When that happened, and upon a correct response, participants received the monetary reward (5 € cents). The total *pay-off* in the experiment was, on average €13.50 (SD 0.62, €12.0-14.45), in addition to the usual payment that subjects receive for their participation in experiments.

4.3.B.5 Data recording and analysis

Epochs with recording or motion artifacts and eye blinks were excluded from analysis using a peak-to-peak threshold criterion (M= 3.07fT, SD=0.22ft, range= 2.8 -3.3fT). Grand averages were calculated on correct and non-rewarded trials according to four probe conditions: control [C], target [T], reward [R], and target_reward [TR]. Event-Related Magnetic Fields (ERMF) waveforms were averaged and plotted using ERPSS software (Event-Related Potential Software System, University of California, San Diego, La Jolla CA, USA). Brain signals were analyzed as a function of probe conditions and task-difficulty. A 2x4 repeated measures analysis of variance (ranova) using the factors difficulty (easy and hard) and probe-

condition (control, target, reward, and target_reward) was conducted. Whenever the ranova test was significant, *posthoc* pair-comparisons among probe-conditions were performed.

4.3.B.6 Behavioral Results

The Mean and standard deviation of task-accuracy and response time were calculated. 2x4 ranova was performed with the factors task-difficulty and probe-condition. Post-hoc pair-wise comparisons were adjusted using Bonferroni correction (n=6, p_{corr}=0.0083). For accuracy, main effects of difficulty, F (1,17) =148.48, p < 0.001, probe-condition F (3,51)=4.358, p < 0.01 and an interaction effect between difficulty and probe-condition F (3,51)=3.40, p < 0.05 were found. Overall, the response in easy trials (M=93.61, SE= 0.68) was more accurate than in hard trials (M=80.67, SE=1.2). There was no difference between probe-conditions for easy trials, but for the hard trials, the response to R-probes (M=82.7, SE=1.43) was more accurate than the response to TR-probes (M=78.70, SE=1.38), t (17) = 4.36, (p < 0.001) (figure 4.14a).

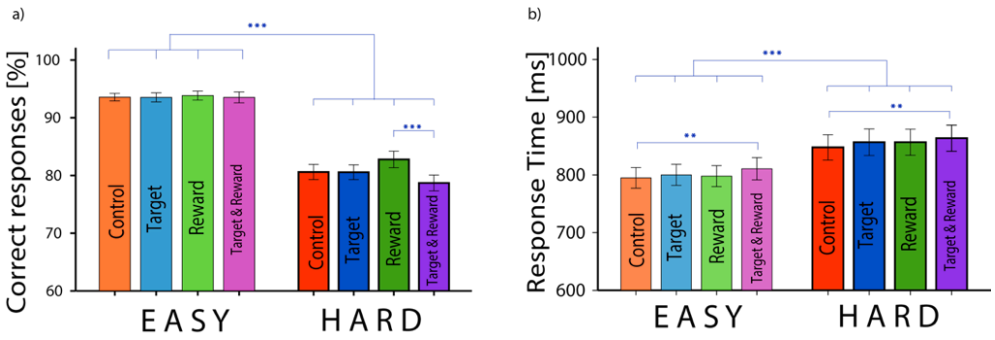

Figure 4.14 a) Bars show response-accuracy according to probe-conditions separated for easy and hard levels. In b bar graphs, the plot response time (RTs) for correct response trials separated for easy and hard level and probe-conditions. Error bars are ± 1 s.e.m., * p<0.05, ** p<0.01, *** p<0.001.

The ranova for response time revealed a significant main effect of task's difficulty F (1,17) =47.90, p < 0.001 and probe-conditions F (3,51) =11.04, p< 0.001, but no interaction effect between task-difficulty and probe-conditions F (3,51) =0.40, p= 0.75. Overall, response time in easy trials (M= 800.77, SE=18.21) was faster than in hard trials (M= 856.00, SE= 22.46). *Post hoc* pairwise comparisons between conditions in easy trials indicated that subjects were slower in TR-probes (M=810.51, SE=19.3) relative to the control probes (M=794.79, SE=17.7) t (17) = -4.384, p < 0.001. In hard trials, the response to TR-probes (M=863.51, SE=22.66) was slower than the response to control probes (M=847.53, SE=21.97), t (17) = -3.97, (p < 0.001) (figure 4.14b).

Additionally, the effect of reward on performance was validated. Statistical analysis comparing the behavioral performance between rewarded-trials and non-rewarded trials was conducted. The rewarded trials were not included in the MEG analysis to avoid confounding reward relevance with reward delivery. A 2x2x3 ranova was conducted, with the factors: reward (rewarded- and non-rewarded trials), task-difficulty (easy and hard), and probe-condition (control, target, and reward probes). Here, in the rewarded trials, there were no T&R probes. The ranova revealed a main effect of reward (F (1,17) =8.43, p= 0.01), reflecting the fact that the response to non-rewarded trials was more accurate than the response to actually rewarded trials. The main effect of task difficulty was replicated (F (1,17) =138.67, p < 0.001), the response on easy trials (M=91.92, SE= 0.90) was more accurate than on hard trials (M=80.30, SE= 1.2). No significant effect of condition (F (2,34) =0.043, p = 0.96) was

found and none of the possible interactions was significant. Regarding response time, main effects of difficulty ($F(1,17) = 39.58$, $p < 0.001$) and type of trials ($F(1,17) = 14.29$, $p = 0.01$) were significant. Subjects were faster on easy trials (M= 816.94ms, SE=18.77) than on hard trials (M= 868.27 ms, SE=23.97), and the response was also faster on non-rewarded trials (M= 825.50ms, SE=19.89) than on the rewarded trials (M= 859.69 ms, SE=23.20). Again, no significant interaction was found.

4.3.B.7 Neurophysiological data

Magnetic responses were analyzed according to probe-conditions and task-difficulty in the non-rewarded trials. Figure 4.15 shows the waveforms for Control-probes (black dash lines), Target-probes (blue lines), Reward-probes (green lines), and TR-probes (lilac lines) for easy trials in the upper panel (4.15a) and hard trials in the lower panel (figure 4.15b). Figure 4.15c shows difference waveforms of T-C, R-C, and TR-C for easy (upper part) and hard trials (lower-part). Waveforms are the average response over six pairs of collapsed sensors located contralateral to the probe and covering the maximum effluxes (red lines) and influxes (blue lines) of the magnetic field.

A sliding-window 2x4 ranova (see general Methods) with task-difficulty (easy vs. hard) and probe-conditions (control, target, reward, and target-reward) as factors revealed that the response to probes varied as a function of difficulty and probe condition (interaction effect) during the time range of 193-288ms, 301-349ms, and 362-416ms (dark blue lines below waveforms). Task difficulty was significant during the time range of 142-191ms and 230-282ms (sky-blue lines below waveforms).

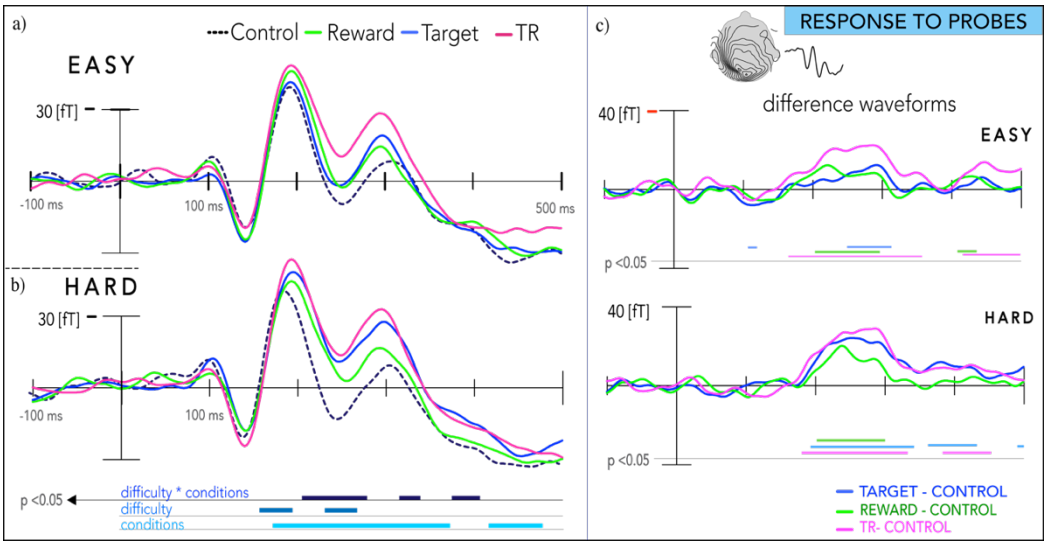

Figure 4.15 ab show the waveforms elicited by easy and hard trials according to probe-conditions plotted in different colors: control (dashed-black-lines), target (blue), reward (green), and target and reward (TR lilac). Significant interaction effects (probe-condition * task difficulty) are highlighted in the lower part of the waveforms with a dark-blue line. The main effects of task difficulty (sky-blue line) and probe-conditions (turquoise line) are also marked. C) Difference waveforms T-C probes, R-C probes, and TR-C probes are plotted separately by difficulty. Statistical significance is marked with a color bar below the difference waveforms: target vs. control (blue), reward vs. control (green), and TR vs. control probes (lilac).

Likewise, probe-condition was significant during 163-380ms and 403-482ms (turquoise lines below waveforms in figure 4.15a and 4.15b). In easy trials, pair-wise comparisons between each type of probe versus control-condition [C] revealed a larger response in target-probes [T] during the time range 95-135msm and ~240-325 ms, from ~191-309ms and 397-451ms for reward-probes [R], and during 152-372ms and 405-500ms for TR-probes. In hard trials, the response to target-probes [T] was larger during

177-343ms, 354-445ms, and 478-50ms, for reward probes [R] during 187-313ms and TR-probes during 165-345ms, 368-467ms relative to hard-control-probes [C]. Overall, Target, Reward, and TR probes elicited global response enhancements with respect to control-probes under both levels of difficulty.

Testing whether task difficulty produces a general enhancement in all probes conditions or whether it induces a selective effect only for target-probes was done by comparing the easy versus hard trials for each probe-condition type (figure 4.16 a-d). Supporting the main hypothesis, only the response to target-probes increased significantly as a function of task difficulty during the time of interest (~170-330ms figure 4.16b; blue lines). Any other response such as control-probes (black lines), reward–probes (green-lines), or TR-probes (lilac lines) increased significantly as a function of task difficulty during the time of interest (figure 4.16a,b, d).

Post-hoc pair-wise comparisons conducted for each probe-condition confirm the significant difference between easy versus hard target-probes during 87-140ms and 193-396ms (sky-blue-shadow areas in figure 4.16b). TR-probes were only different during the late time range (476ms-500ms). No other comparison between easy and hard trials was significant. Thus, increasing the difficulty of the task selectively enhanced the response to target-probes during the time range where the GCBA response (170-330ms) appears.

Additionally, Target- and Reward-probes were compared as a function of difficulty when they were presented together (TR-C probes "combined response") relative to when they were presented alone but added offline "added-TR-response" = ([T-C probes] + [R-C probes]) (figure 4.16e). As seen in the bar graph in figure 4.16f, the mean of the magnetic response during the time-range of significance (191-293ms) was roughly additive between the target-probes and reward probes in the easy condition as previously reported by Hopf et al., (2015), but not for hard trials (figure 4.16f).

A 2x2 ranova comparing "combined-TR response" (TR-probes) versus "added-TR-response" as a function of difficulty (easy vs. hard) revealed an interaction effect between the time range of 110-160ms, 201- 290ms and 293-353ms. Later, pair-wise comparisons for added vs. combined TR-response showed that in easy trials there was no difference between added and combined, but in hard trials, the response was larger for the added relative to the combined TR-response (193-290ms). This data confirmed that while in the easy condition, the relationship between target-and reward-response was additive, in the hard condition, such a relationship was not preserved.

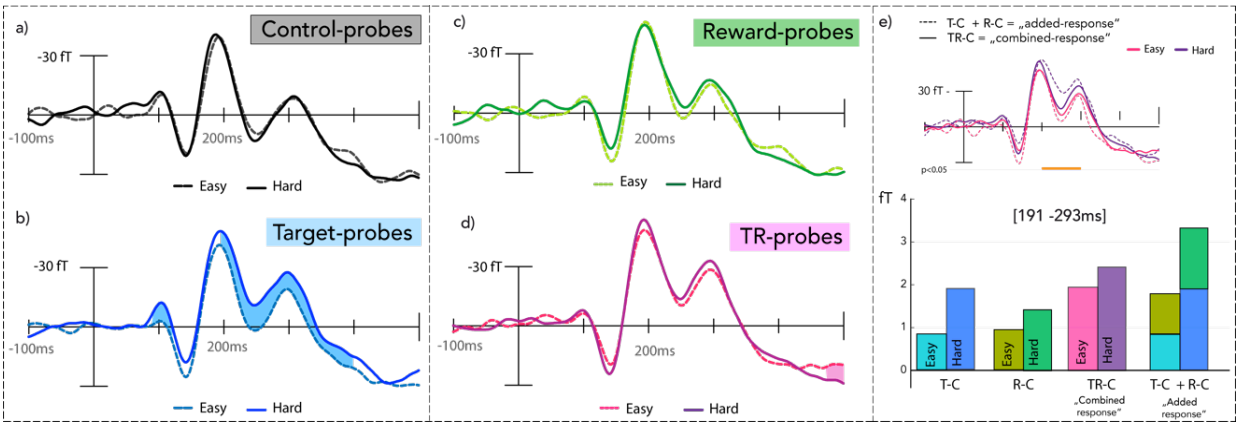

Figure 4.16. From a to d, the waveforms to probe conditions are illustrated. A shows control-probes for easy trials (dash-black line) and hard trials (black line). B shows the response to target-probes for easy (dash-sky-blue lines) and hard trials (dark-blue lines). C shows the response to reward-probes for easy (dash-light-green lines) and hard trials (dark-green lines). D shows the response to target-reward-probes [TR] for easy (dash-lilac) and hard trials (dark-lilac). E and f show the mean amplitude response during 191-293ms to the four-probe conditions according to the level of task difficulty, and also the TR-added condition relative to the TR-combined.

4.3.B.8 Conclusions

Indices of global color-based selection were observed for task-related and reward-related colors beginning at ~190-and lasting to ~330ms stimulus onset in both levels of difficulty: easy and hard. Increasing the task load led to an enhanced selective response to target-probes, but not to other probes types, including the R-probe, TR-probe, and C-probe, suggesting that GFBA and GRBS responses in visual cortical areas operate independently at the top-down level.

The additive relation between T-probes and R-probes in the easy condition was also replicated. Nevertheless, the response to TR-probes in the hard condition did not increase proportionally as the single T-probes response did. While this unexpected result does not contradict the central hypothesis, it remains unclear why TR did not increase as a function of difficulty. Based on the current data, it is not possible solving this issue, but some plausible testable hypotheses for future research are provided. They are offered here and later discussed in more detailed in the discussion section:

The TR-probe response did not increase in the hard condition because:

1. The maximum increment (ceiling point) was already reached.

2. The TR-color combination signaled reward instead of single-reward related color. Since the rewarded trials coincide with the trials where target and reward appeared together in the focus of attention, it is possible that subjects coded the TR combination as the instance being associated with reward delivery and not the R color alone. Then as the reward was kept fixed in easy and hard conditions, the response to TR-probe was almost the same.

4.4 Experiment 4

As described in the introduction section, the attentional selection is not only based on the task demands at hand but also influenced by the past selection history of features. Previous studies have shown that the selection of locations, colors, orientations, shapes, objects, and faces is facilitated when those features have been attended in the past (Becker, 2008b; Becker et al., 2014; Bichot & Schall, 1999, 2002; Goolsby et al., 2001; Henson, 2003; Henson et al., 2004; Henson et al., 2000; Maljkovic & Nakayama, 1994, 1996; Müller et al., 2000) or when they have been previously related to reward (Anderson et al., 2011; Anderson & Yantis, 2013; Hickey et al., 2014; Pollmann et al., 2016; Sharifian et al., 2017). However, when the reward-associated features or objects are displayed as part of distractor items, they can impair performance (lower accuracy and longer RTs) (Anderson et al., 2011; Chelazzi et al., 2014; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a, 2010b; Kristjánsson et al., 2010; Theeuwes, 1994). The acquired relevance gained by reward-related features can persist over longer periods (weeks or months) even when they become reward-irrelevant (Anderson & Yantis, 2013; Della Libera & Chelazzi, 2009).

While experiment 3 compared reward-based and attention-based selection when relevant features (colors) are explicitly defined. This experiment aims to test whether primed colors (past targets and past reward-related colors, implicit bias) would elicit a different GCBA/GFBA response than explicitly task-relevant colors (target reward color in a current trial or block) relative to unprimed control colors. To this end, we use the unattended probe paradigm to compare the probe response elicited by past attended or rewarded colors (primed colors), currently attended or rewarded colors (match target or reward colors) and neutral colors (control colors).

4.4.1 Subjects

Nineteen (mean age=26.63, SD=4.5, range=20-38 years) students from the Otto von Guericke University participated in this experiment. All participants gave their informed and written consent, and they were compensated for their participation (8 € per hour). All subjects were right-handed, and nine of them were women. All subjects reported normal or corrected to normal vision.

4.4.2 Stimuli

Stimuli were two circles displayed in the lower quadrants of the left and right visual fields on a gray background (10 cd/m^2). Six colors were used as the target, reward, or control colors in the experiment: red, green, blue, magenta, cyan, and yellow. Color assignment for the target, reward, or control condition changed over blocks, with each color serving as the target or reward only once (one block) during the whole experiment. There were three additional distractor colors (orange, violet, and gray) presented only in the attended circle in combination with the target, reward color, or another distractor color. As we see in figure 4.17a, there was a four-color combination in the attended circle: Target + distractor, Reward+ distractor, Target + Reward, and distractor + distractor. The distractor colors (orange, violet, and gray) were irrelevant for the task, and they were the same in all blocks and across subjects. In total, nine colors were used. Those colors were isoluminant (mean= 20.710 cd/m^2) psychophysically matched using the method of flicker-based luminance matching (Lee, Martin, &

Valberg, 1988). Stimuli were created and presented using MATLAB release 2009b, The Mathworks, Inc., Natick, Massachusetts, United States, and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

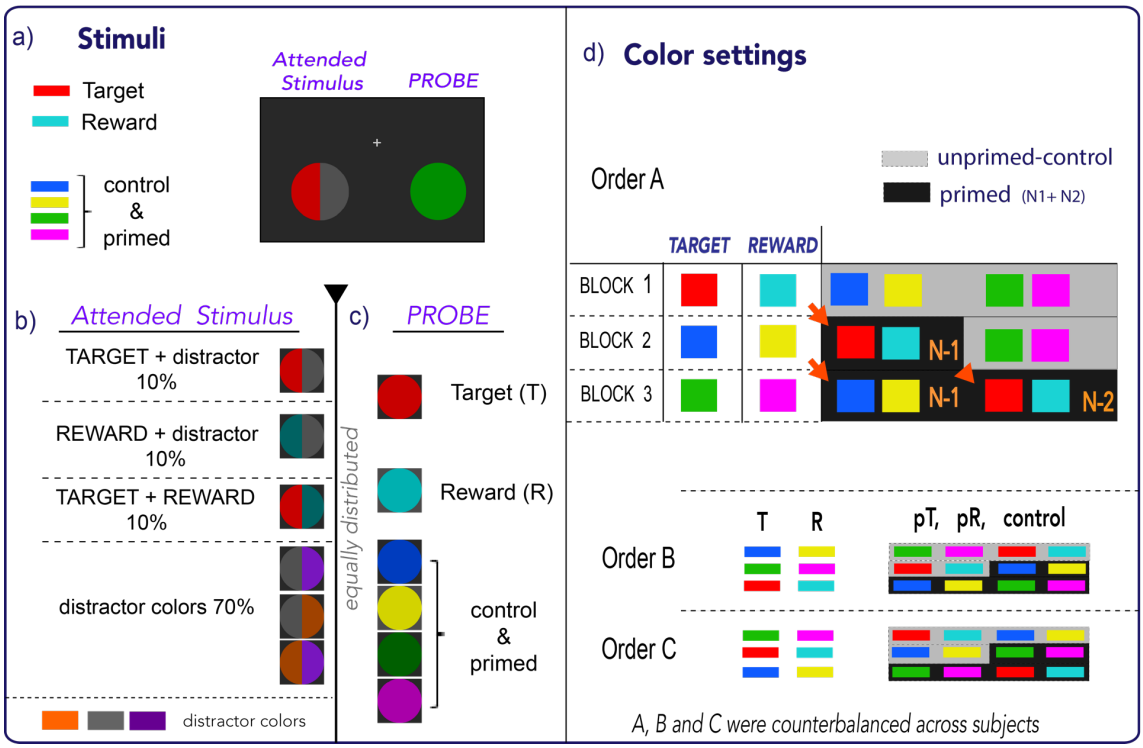

Figure 4.17a Stimuli consisted of two-colored circles displayed in the low quadrants of the screen. b) Attended circle was colored either with the target, reward, or distractor colors. c) Probe stimulus was a full colored circle drawn in target, reward, or control colors (primed and unprimed). d) Color settings show color assignments for target, reward, and control colors on each block and over the experiment. Control color consisted of unprimed colors (never been target or reward before; they are marked with a light gray area) and primed target or primed reward colors: those colors that have been target or reward-related in the previous block (N-1) or two blocks back (N-2). There were three color-assignment orders: A, B, C counterbalanced across subjects.

4.4.2.1 Attended stimuli (TARGET-circle)

The circle displayed on the left side was always the attended circle. It was a divided into two halves and, each half was assigned to the target, reward or distractor color as follows: Target and distractor color (10% of trials), reward-related color and distractor color (10% of trials), target and reward color (10% of trials) and two distractor colors together (70% of trials). Reward color was presented as frequent as the target color in the attended circle (figure 4.17 a-b).

4.4.2.2 Probe stimuli and probe conditions

The probe stimulus was a unicolor circle always displayed on the right side and filled with one out of the six colors: red, green, blue, magenta, cyan, and yellow. Each color had the same frequency of presentation, and their order was randomized (figure 4.17a-c, ~16.6%).

There were three target colors and three reward-related colors in the experiment. Before being target or reward, each color appeared as unprimed-control color, except for the first target and reward color

(block 1), which never served as unprimed-control color. After being target or reward, each color became primed target or primed reward respectively in the subsequent blocks (figure 4.17d), thereby forming the following probe-conditions: Target (T), Reward (R), Unprimed-control (C), Primed-Target (pT) and Primed-Reward (pR).

Three block-schedules were designed to assign the order of color's presentation. These three schedules were counterbalanced across subjects (See figure 4.17d).

Figure 4.18b illustrates the probe conditions during the task using the order A. In block one, red was the target color and cyan the reward-related color. In contrast, blue, yellow, green, and magenta were unprimed-control colors. In the second block, a new target (blue) and reward color (yellow) were assigned. Green and magenta remained as unprimed-control colors while red and cyan became primed-target color (N-1) and primed-reward color (N-1), respectively. In the third block , green was the target and magenta reward-related color; blue became primed-target color (N-1), yellow primed-reward color (N-1), red remained as primed-target color (N-2) and cyan as primed-reward color (N-2).

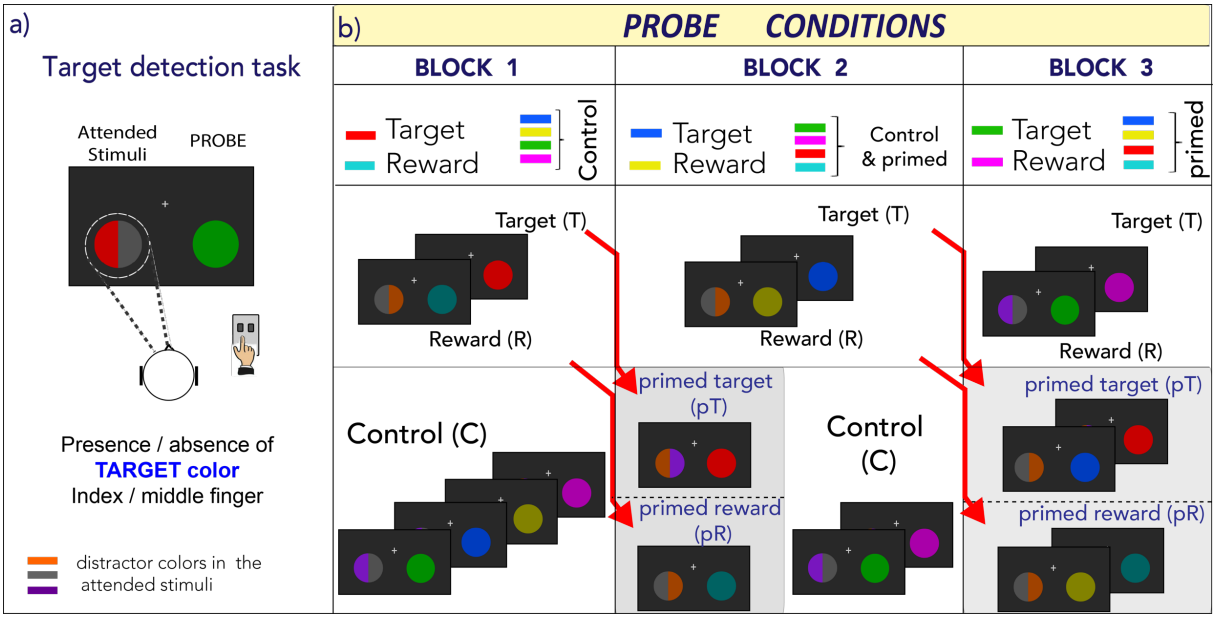

Figure 4.18. a) Subjects performed a target detection task where they had to indicate whether the target color was or not on the attended circle by pressing their index or middle finger (counterbalanced across subjects). B shows a schematic illustration of probe-conditions according to color settings on each block for the order "A" as an example.

4.4.3 Task

Subjects performed a target detection task. They had to covertly attend the circle on the left side while fixating at the center (fixation cross) to indicate whether the target color was present or absent in the attended circle. Each trial consisted of two circles (target and probe) displayed in the lower quadrants for 300ms, followed by a blank period of 800-1300ms (uniform distribution). On rewarded trials (20% of total), there was an additional feedback frame presented by 400ms informing about the gained reward ("5 cents" or "0 cents") and followed by another blank period of 600-900ms (uniform distribution). Participants gave their response within a time window of 1100ms by pressing one or another button using the index or middle finger for target-presence and target-absence (counterbalanced across subjects).

The total of 2160 trials was blocked by target and reward color and organized in three main blocks divided into two parts, each block to allow subjects blinking and resting the eyes. Five small pauses were lasting for ~ 30s within each set.

4.4.4 Reward Schedule

Participants received the monetary reward (5-euro cents= € 0.05) whenever they gave a correct response to trials where the current reward-related color was presented in the attended circle either in combination with the target or with a distractor color (20 % of total trials). The total *pay-off* for each subject was on average €18.83 (SD= 1.76) in addition to the usual payment for their participation in experiments (8€ per hour).

4.4.5 Data recording and analysis

Brain signals were acquired recording the MEG signal. The continuous signal was online filtered with a band-pass filter of 0.01- 300Hz and digitized at a sampling rate of 1000 Hz. (During offline preprocessing, data was down-sampled to 500Hz). Environmental noise was canceled by applying signal space separation [SSS] (Taulu & Simola, 2006; Taulu et al., 2004) using Elekta Neuromag® SSS Maxfilter™ software. Grand averages were calculated for correct, non-rewarded target absent trials only. According to color assignments to the probe, the following conditions were computed: target, reward, primed target, primed reward, and control.

ERMF waveforms were calculated using Fieldtrip Toolbox (as described in the methods section above) (Oostenveld et al., 2011) and exported to ERPSS software for plotting and statistical analysis (Event-Related Potential Software System, University of California, San Diego, La Jolla CA, USA).

4.4.6 Behavioral Results

Task performance was indexed by task accuracy (proportion of correct response) and response time (ms) and first analyzed according to the type of trials. Then, the analysis focused on non-target and non-reward trials as a function of probe conditions.

As visible in figure 4.1a, task accuracy ($F(3, 54) = 22.78$, $p < 0.001$) and response time ($F(3, 54) = 53.60$, $p < 0.001$) varied depending on the type of trials. Responses to trials when target and reward were absent were the fastest (M=575ms, SD=89ms) and the most accurate (M=97.69, SD=1.91) in comparison to target-present trials (Acc: M=79.72, SD=13.9; RT: M=742ms, SD=90ms), reward-present trials (Acc: M=92.1, SD=4.55; RT: M=653ms, SD=115ms), and Target_+_Reward present trials (Acc: M=85.46, SD=10.9ms; RT: M=720ms, SD=80ms).

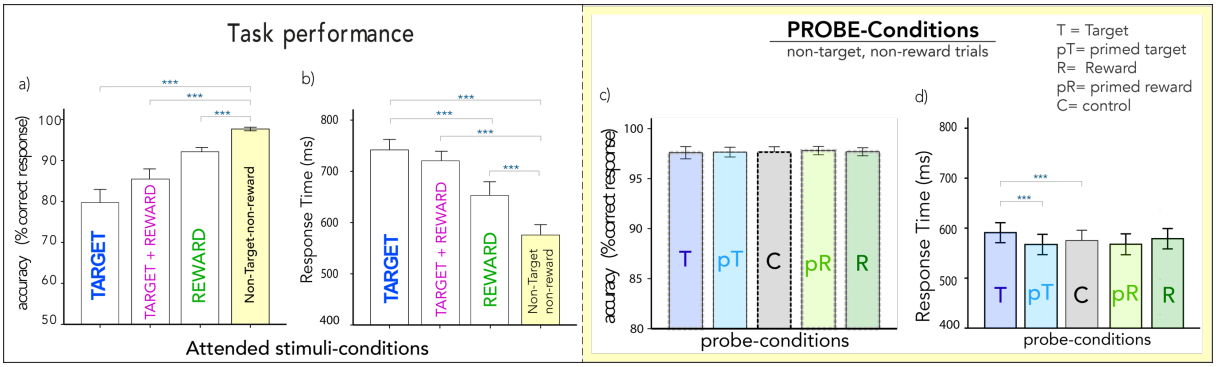

Figure 4.19a Mean percentage of correct responses and response time are plotted according to colors presented in the attended circle. b) Bar graphs show the response accuracy and response time according to probe-conditions for trials where only distractors were presented in the attended stimuli (trials in yellow in graphs a and b). Error bars are + 1 s.e.m. ; * p-value < 0.05, ** p-value < .01, *** p-value < .001.

Task performance was analyzed as a function of probe-conditions. The analysis was focused on non-target and non-rewarded trials only (trials where neither the target nor the reward were presented in the attended circle; yellow bar in figure 4.19ab). A one-way ranova 3-levels was conducted to compare the control trials (M=97.7ms, SD=1.77ms), primed-trials ([pT and pR]; M=97.73ms, SD=2.04ms) and target and reward trials (T and R; M=97.63, SD=2.31) for accuracy and response time separately. Ranova revealed no difference in accuracy ($F(2, 36) = 0.065$, $p = 0.937$) but a significant difference in response time ($F(2, 36) = 4.80$, $p = 0.014$) between those conditions. No difference was observed between control (M=575ms, SD=93) and primed colors ([pT and pR]; M=568ms, SD=90ms), but Target and Reward ([T, R]; M=585ms, SD=87ms) required more time than primed colors ([pT and pR]; $t_{[18]} = -3.4$, p=0.003) and control probes ($t_{[18]} = 2.93$, $p = 0.009$).
By splitting priming trials into primed-target and primed-reward, and current target and current reward, the response to target probes was slower (Target; RT: M=590ms; SD= 87ms) than primed-target (M=567ms; SD= 89ms; $t_{[18]}=-4.127$, p=0.001), primed-reward (M=568ms; SD= 91; $t_{[18]}=-4.15$, p=0.001) and control trials (M=579ms; SD= 85; $t_{[18]}=3.56$, p=0.002).

4.4.7Neurophysiological data

Brain signals were analyzed comparing the response to probes on non-target and non-reward trials depending on whether the probe-color was the target, reward, primed target, primed reward, or control colors.

4.4.7.1 Response to target probes

Figure 4.20 shows two sets of waveforms corresponding to two processes associated with the target; the early one when target-priming bias arises, and the late one, in extrastriate visual areas, when the global color-based selection response appears. As in the previous experiments, the waveforms represent the probe response averaged across selected sensors, after collapsing the efflux-influx components of the magnetic response (see methods). As illustrated in magnetic field maps in figure 4.20d and 4.20h, the selected sensors are marked with black dots and correspond to those sensors located contralateral to the probe with the maximum response at the time of interest.

Figure 4.20a shows the initial enhanced probe response to primed-target colors (solid light blue) relative to control colors (solid black lines), and an enhanced response to target colors (solid dark blue lines) relative to control colors (solid black lines). A sliding window one-way ranova (3-levels) comparing the three probe responses [target vs. primed-target vs. control] validated a significant probe-type effect in the time range of 48-78ms, 84-114ms, 174-214ms and 370-422ms (black bar below waveforms). The posthoc pairwise comparison between primed target and control colors revealed significant differences during 42-80ms and 76-112ms (light blue bar). Similarly, the contrast between target colors and control colors showed a significant difference during 40-80ms, 86-120ms, 166-208ms, and 464-500ms (blue bar). No differences were found between target minus control (T-C; dash dark blue lines in figure 4.20b) and primed target minus control (pT- C; dashed light blue lines in figure 4.20b) in the early time range, but differences appeared during 168ms-220ms and 372-424ms, as visible in figure 4.20b.

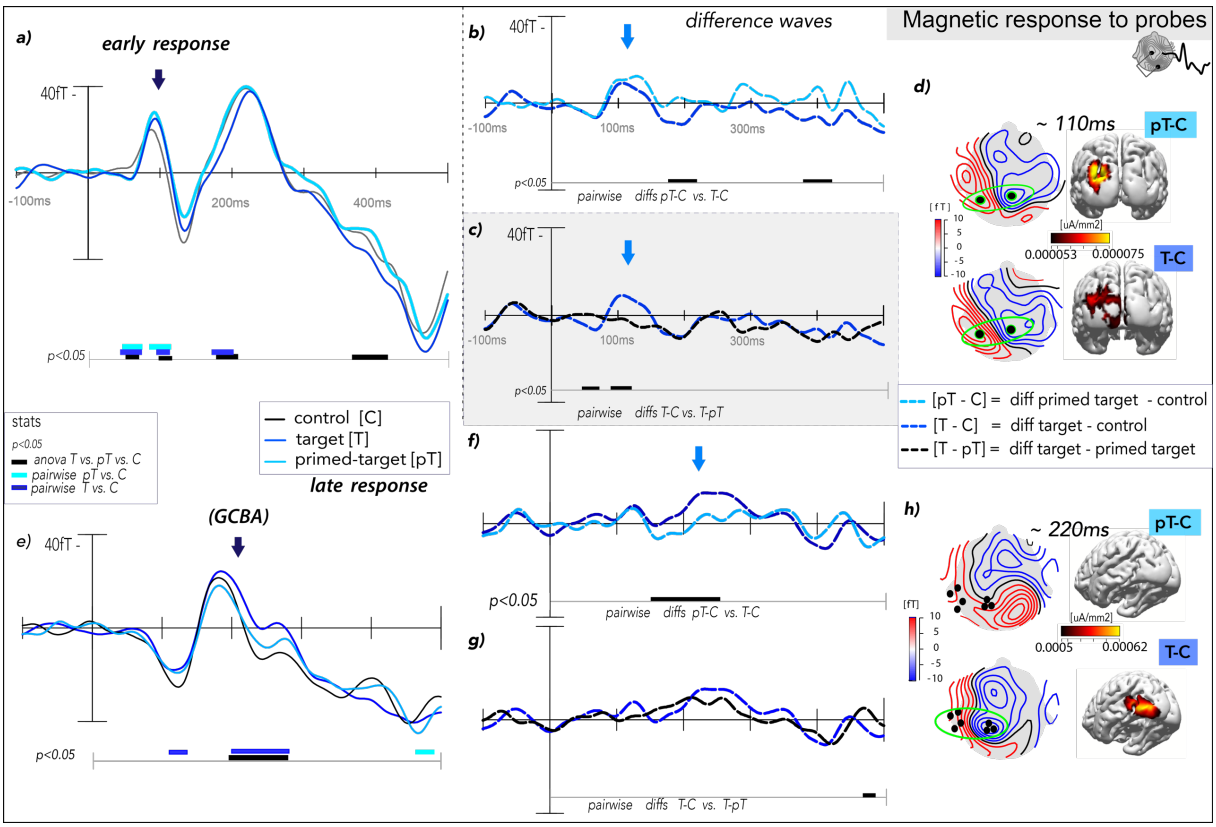

Figure 4.20. Magnetic response to probes comparing primed-target colors (light blue line), target trials (dark blue lines), and control colors (black lines) response. A and e show the waveforms to primed target, target, and control color responses. B and c show the difference waveforms to T-C relative to pT-C. F and g show the difference waveforms to T-C relative to T-pT. D and h illustrate the magnetic field distribution of the difference-responses and the CSDs associated with them. The horizontal lines under the waveforms indicate the significance ($p<0.05$) for the ranova (black) and pair-wise comparisons.

Magnetic field distributions (efflux-influx: red-blue maps) and the corresponding source localization (CSD: current source densities computed in Curry 7 using the MNLS method) at selected time points are shown in figure 4.20d for the early response and in figure 4.20h for the late response. The early response localizes to parietal regions. The late response, the global color-based selection response, is localized in extrastriate visual regions. Given that the magnetic field distribution and current source

density estimates differed between the responses in the early and late time-range, different sensors were used to analyze the global color-based response in those time-ranges.

As shown in figure 4.20e-h, the waveforms for GFBA correspond to sensors located contralateral to the probe with the maximum magnetic strength appearing roughly at ~220ms. Figure 4.20e plots the waveforms to target (dark blue), primed-target (light blue), and control probes (black). Here, the target probe response was significantly larger than the control probes during 196-286ms, while the slight enhancement for primed-target probes relative to control probes in this time was not significant.

A one-way ranova (3-levels) comparing target-probes, primed target-probes, and control color-probes validated the significant probe-type effect from 192-274ms. *Post-hoc* pairwise comparisons confirmed a non-significant difference between primed-target relative to control color, but a clear difference between target versus control color during the time range 110-138ms and 196-286ms. Pairwise comparison between T-C versus pT-C responses validated a difference in the time range between 180-230ms and 372-404ms (figure 4.20f).

Additionally, figures 4.20c and 4.20g show two difference-waveforms to target probes, one when it is subtracted from control colors (dashed dark blue line) and the second subtracted from primed target colors (dashed black line) for the early and late response, respectively. The T-pT comparison is relevant because most of the studies investigating GFBA effects, typically contrast the target response relative to primed target colors since the previous target colors are used as control colors in the subsequent blocks. As seen in figure 4.20c, when comparing T relative to pT, no early modulation was observed as it appeared in T relative to C. This difference between both difference-responses T-C and T-pT was statistically validated during 42-60ms and 76-92ms when performing a pairwise comparison (T-C vs. T-pT).
A similar comparison was performed between waveform modulations reflecting the late GFBA response, as seen in figure 4.20g. Here, no significant difference was observed between T-C versus T-pT.

4.4.7.2 Response to reward-color probes

Similar comparisons were conducted for past reward and currently reward-related colors relative to unprimed control colors. Here, the early reward response displays two early processes. The first was localized contralateral to the probe side. And the second was localized contralateral to the target side. Thus, two sets of different sensors were selected to pick up the maximum magnetic strength for each response. For the late global reward-based selection response (> ~200ms) contralateral to the probe, the third set of sensors was selected. Sensors, marked with a black dot in the magnetic field distributions, were selected based on the maximum response at the time of interest (visible in figure 4.21e, 4.21f, and 4.21i). Figure 4.21a-d shows the waveforms for the early response. Figure 4.21g-h shows the late response; magnetic field distributions and CSDs are shown in 4.21e and g.

The first response arising from visual cortices is enhanced to primed-reward colors (pR) relative to control colors, but no to current reward (R) relative to control colors at this time. Later, roughly at ~100ms, the response to reward-related colors is enhanced relative to control. A one-way ranova (3-levels) comparing these three probe-conditions [reward vs. primed reward vs. unprimed control]

revealed a significant effect of type of probe (blue line in the waveforms) at 28-74ms and 108-120ms. *Post-hoc* pairwise comparisons validated that the response to primed reward colors differed from control colors during the time range of 26-78ms and 306-342ms (gray bars under the waves). The reward probe-response relative to control was significantly different during the time range of 108-124ms and 248-282ms (dark green bars under the waves). A significant difference was found when comparing the two difference-responses R-C and pR-C probes at 28-52ms, 104-122ms, and 252-260ms.

The second response shown in figure 4.21c-f (contralateral to target stimuli) was similar to primed-reward and reward colors. A one-way ranova (3-levels) for these three probe-conditions [reward vs. primed reward vs. control] revealed a significant effect of type of probe (black bars under the waveforms) at 76-114ms and 216-250ms. *Post-hoc* pairwise comparisons validated that the response to primed reward colors was different from the response to unprimed colors during the time range of 72-114ms and 214-254ms. The reward response relative to unprimed control was also significantly different during the time range of 80-118ms. No difference was found when comparing the two response differences R-C and pR-C.

As previously done for the target probes, the response difference reward-minus-control (R-C) was compared with the difference reward-minus-primed reward (R-pR). As shown in figure 4.21d, the reward probe is enhanced when subtracted from control colors, but not when it is subtracted from primed reward colors. This difference was validated using a pairwise comparison, which was significant during the time range of 72-94ms and 214-234ms (statistical significance is marked with yellow lines under the difference waves in figure 4.21d).

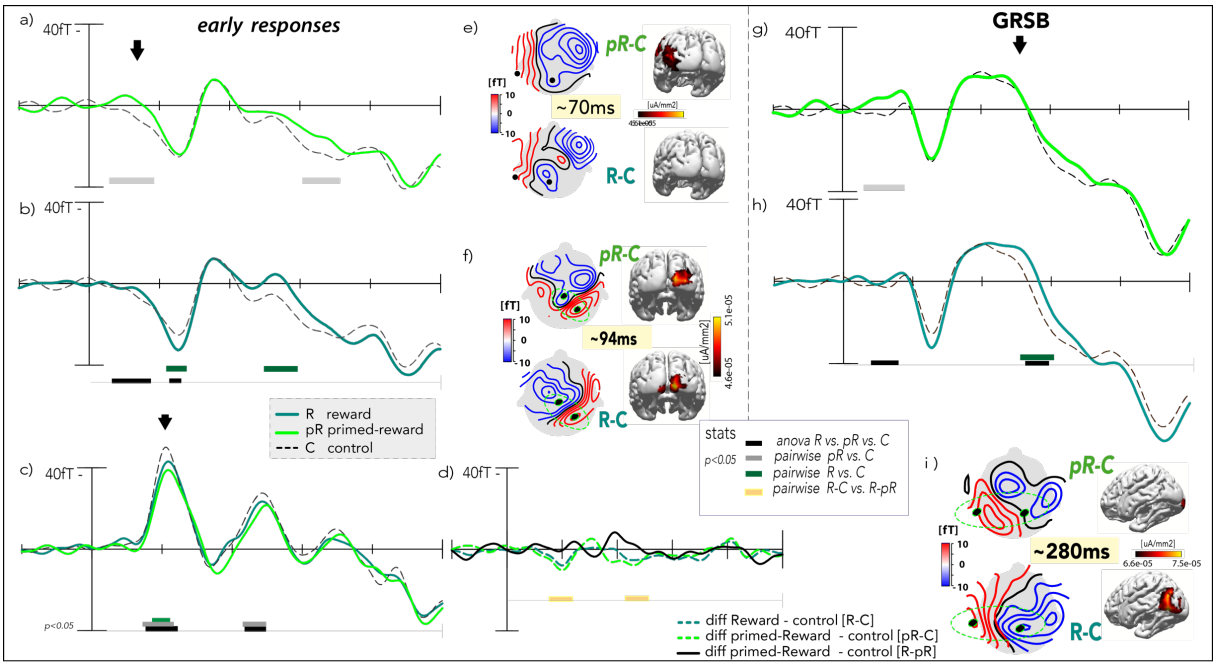

Figure 4.21 Magnetic response to primed-reward colors (light green lines), reward trials (dark green lines), and control colors (dashed black lines) are shown in a-d and g and h. The response differences plotted are reward minus control (R-C; dashed dark green lines), primed reward minus control (pR-C; dashed light green lines), and reward minus primed reward (R-pR; solid black lines). In e, f and i the magnetic field distribution and current source estimates for the response difference-responses reward minus control [R-C] and primed reward minus control [pR- C] are shown. Colored bars below the waveforms corresponded to the

time range when the statistical difference between conditions was significant ($p<0.05$) for ranova (black) and pair-wise comparisons (gray, green, and orange).

The late global reward-based response arising from extrastriate visual areas after ~200ms is shown in figure 4.21e. As visible, the strongest magnetic response is contralateral to the probe; thus, the sensors with the maximum response at this site were selected for the analysis.

The reward probe response was larger than the response to primed reward probes roughly after ~200ms. By comparing the three types of probes conditions (R, pR, and control), the ranova revealed a significant effect of the type of probe during the time range of 32-88ms and 258-294ms. The pairwise comparisons between reward and control colors validated a significant effect during the time range of 252-304ms fitting with the time where typically the GRBS appears. Interestingly, the primed-reward response differed from control color probes only in the time range of 26-92ms (see figure 4.21 g), but not later on, suggesting that the late GRBS response is elicited only by the current reward color. The pairwise comparison between the response differences (R-C vs. pR-C) confirmed this; both difference-responses varied between them at three time ranges 32-72ms, 110-144ms, and from 252-294ms.

Figure 4.21e, f, and i show the magnetic field distributions (efflux-influx: red-blue maps) and the corresponding source localization roughly at ~70 ms, ~94ms and ~ 280ms. The earliest modulation appears in visual areas contralateral to probe; then, it moves to an area contralateral to the attended side (~94ms). The maximum late response (R-C) occurs between 258-294ms in the extrastriate visual areas contralateral to the probe.

4.4.8 Conclusions

Taken together, the task-irrelevant but previously attended and rewarded colors elicit initial modulations in parietal and visual cortices. These early responses likely reflect a neural correlate of an immediate and implicit sensory bias to all-relevant colors, including the current and past targets. This very early response does not differentiate between whether the color is the current target or a previously attended color, suggesting that the implicit bias must build up within trial-blocks. Regarding reward colors, there is a rapid response enhancement in extrastriate visual areas for primed reward relative to current reward. No difference between them is visible in the following early processing stages. Finally, primed target and primed reward colors do not elicit a significant GFBA or GRBS response.

V. GENERAL DISCUSSION

5.1 Experiment 1

5.1.1 The Temporal dynamics of GCBA is not altered by continuous attention to the attended color.

Experiment one tested whether a stimulation-driven (i.e., feedforward) bias for the attended color by continuous color-stream presentation would alter the temporal dynamics of the GCBA reflected by a modulation of the feedforward sweep of information processing in the visual system. There is considerable empirical evidence for feature selection to operate in a spatially global manner (Andersen et al., 2013; Bartsch et al., 2015; Bondarenko et al., 2012; Martinez-Trujillo & Treue, 2004, 2005; Maunsell & Treue, 2006; Mcadams & Maunsell, 2000; Moher et al., 2014; Saenz et al., 2002; Sàenz et al., 2003; Stoppel et al., 2012; Treue & Martinez-Trujillo, 1999; Zhang & Luck, 2009). However, there is still a controversy about the temporal locus and cortical level of selection underlying GFBA. Zhang & Luck (2009) and Moher et al., (2014) have reported ERP indices of GCBA appearing at 80-130ms after stimulus onset in the form of a modulation of the amplitude of the P1 wave (~100ms). The early onset of GFBA effects was taken to indicate that GCBA modulates the feedforward sweep of information processing in the visual system. Such P1 modulation was seen only under conditions of color competition within the focus of attention (Zhang & Luck, 2009). However, Bartsch and colleagues (Bartsch et al., 2015) have reported GCBA effects to appear later, i.e., after ~150ms in the form of modulation of posterior N1 and N2 even without competition in the focus of attention, suggesting that GCBA affects only feedback processing in visual cortex. The conflicting observations could arise from differences in experimental designs. Zhang & Luck (2009) used a continuous stimulus presentation. Continuously attending a flickering color-defined dot group allows us to establish and uphold a continuous feedforward-driven selectivity bias for the attended color before the probe's onset (stimulus-driven preset bias). In experiments using onset stimulation like in Bartsch et al., (2015), the stimulus-driven color representation only appears with probe onset. The top-down color bias, therefore, must be established anew on each trial (no stimulus-driven bottom-up bias). The question here was whether a continuous stimulation-driven preset bias for the attended color would account for the differences in the temporal dynamics of GCBA responses.

The results of experiment one showed that a continuous selectivity bias for the attended color influences the amplitude of the GCBA response, but not the latency at which GCBA modulations first appear. Contrary to the initial prediction, there was no GCBA modulation in a time range reflecting the feedforward sweep of processing in the visual cortex (until ~100ms after stimulus onset). The time course of the GCBA response was rather more in line with Bartsch and coauthors (2015; 2018), who reported GCBA effects to appear beyond ~150ms after stimulus onset. The GCBA responses in experiment one appeared after ~160ms with amplitude maxima around ~190-200ms and ~260-270ms in both, the continuous (preset) and onset (no-preset) condition. Importantly, the response pattern (size of the effect) varied between those conditions in an unexpected way. The first modulation appearing at ~200ms was smaller in the continuous condition than in the onset condition. The later response peak at ~260-270ms was significantly larger for continuous than for the onset condition.

The observation of an amplitude enhancements of the N1 and N2, but not of the early P1, is overall consistent with several previous studies showing that feature attention (to color, orientation, and motion) is indexed by negative polarity modulations of the ERP referred to as Selection Negativities (SN) (Anllo-Vento & Hillyard, 1996; Harter & Aine, 1984; Hillyard & Munte, 1984). The SN typically arises

from ~ 130ms to 350ms after stimulus onset for attended items relative to unattended ones. SN modulations are considered to reflect feedback signals in the visual cortex. As Harter and Aine suggested (Harter & Aine, 1984), the SN does not index a unitary process, but rather a collection of functional processes (several selection negativities) overlapping in time. The present data and those of recent studies (Bartsch et al., 2015, 2017; Bondarenko et al., 2012) support this proposal in the sense that GCBA is reflected by a sequence of two modulations propagating backward from higher to lower level of representation in visual cortex. These modulations have been associated with two independent cognitive operations, referred to as "template matching" and "discrimination matching" (Bartsch et al., 2015; Bondarenko et al., 2012).

Given that a preset bias for the attended color allowed by the continuous color stream in experiment one is not associated with a modulation of the P1 component, the question remains why some studies have found this early GCBA response, and others have not. One possibility is that feature-priming effects play a role (see experiment 4 below). In Zhang and Luck (2009) and Moher et al., (2014), the colors used as targets (red and green) were not counterbalanced trial-by-trial or block-by-block. Target and distractor color assignments were kept constant over half of the experiment (Zhang & Luck, 2009) or even during the whole experiment (Moher et al., 2014). It may have caused color repetition priming to play a more significant role than usual. In the present experiment, the target color changed on each block, leaving less room for color repetition priming effects. Therefore, the P1 modulation reported by Moher et al., (2014) and Zhang and Luck (2009) may reflect – at least partially - color repetition driven by the sustained consecutive repetition of the target color during the experiment.

Additionally, the interpretation that the P1 effect reflects an enhanced response to the target color, as suggested by Zhang and Luck (2009), has been challenged. Moher et al. (2014) showed that the P1 enhancement for an attended color is only relative to a distractor color, compared to a neutral color, no P1 enhancement was seen. The no P1-enhancement was taken to indicate that GFBA effects in the time range of the feedforward sweep of processing reflect distractor attenuation.

5.1.2 Attenuation of the N1 response

In previous work (Bartsch et al., 2015; Bondarenko et al., 2012), the operation of GFBA was typically reflected by an amplitude enhancement of the N1 and N2 response. Here, we made an unexpected observation. The continuous condition showed a significantly smaller amplitude enhancement in the first phase of the GCBA response (~190-200ms) than in the onset condition. This attenuation comes as a surprise and warrants further consideration.

5.1.2a Low-level sensory adaptation as an account of the N1 attenuation

Continuous color stimulation might lead to a reduced response due to sensory adaptation to the hue-range of the color stream running through in the continuous condition. This attenuation would then be independent of attention. Such an adaptation account is, however, unlikely because a similar adaptation-driven attenuation would be expected when the probe matches the non-target color in the focus of attention (OFF-TARGET physical match). However, no response whatsoever was observed in the N1 time range between the OFF-TARGET physical match and non-match condition (see figure 4.3b-d, black lines). Thus, the attenuation of the probe response in the continuous condition is unlikely to reflect color adaptation.

5.1.2b The N1 attenuation reflects distractor suppression.

The N1 modulation, alternatively, might reflect distractor suppression (Gaspelin & Luck, 2018) instead of a GCBA response. Given that the target probe contains the relevant color, it interferes with the color selection in the focus of attention. In the continuous condition, attending the continuous color stream demands more resources in the FOA because the discrimination requires a higher resolution of color discrimination to identify the point where the target color is reached. This may require more distractor suppression (probe suppression) in the continuous versus the onset condition. The N1 attenuation could reflect a relative amplitude reduction due to an overlapping distractor positivity (Pd), which takes away some amplitude from the N1. However, the data from experiment one does not allow verify this possible interpretation. Data from experiment two will allow addressing this issue.

5.1.2c Selective tuning as an account of the N1 attenuation

When the color stream approaches the target color in the continuous condition, the selectivity required to determine the point when the target color is reached increases steadily. This increment may be accomplished by a selective tuning process that prunes away units less optimally tuned to the target color (colors appearing immediately before than target). This inhibition would lead to a reduction of the amplitude of the local field response (measured with ERPs and ERMFs) relative to conditions where the color stream runs through a range of non-target colors (OFF TARGET match condition). This interpretation would endorse the Selective Tuning Model (Tsotsos, 2011; Tsotsos et al., 1995) and is – as further discussed below (experiment 2) – the, here, preferred interpretation.

5.2 Experiment 2

5.2.1 Tuning of the target template representation is reflected by attenuation of the N1 response.

The data from experiment 1 were taken to suggest that continuous attention to the color stream facilitates color selection via selective tuning (Tsotsos, 2011; Tsotsos et al., 1995), which accounts for the attenuation of the GCBA response in the N1 time range when compared with the onset condition. In the onset condition, less tuning was required because the target color separated from widely different non-target colors in color space. The selective tuning model (STM) proposes that sharpening the tuning response for coding the target feature is accomplished by a suppression of the response of units less optimally tuned to the target feature (Tsotsos, 2011; Tsotsos et al., 1995). The population response from a lower number of contributing units is smaller relative to the response of a less tuned population. Such suppression of less-optimally tuned units could, therefore, appear as an attenuation of the N1 response (~200ms). Thus, as illustrated in figure 4.7, selective tuning would be expected to cause a net attenuation of the ERP/ERMF response.

In the second experiment, we asked whether tuning would re-appear under onset conditions (i.e., when no preset-bias is possible) when the target color selection requires discrimination between very similar colors in the same hue range. We expected that color selection would then require selective tuning and result in a relative attenuation of the N1 response. The results of experiment 2 show that high T-D similarity in the focus of attention, the amplitude attenuation of the N1, was observed, as predicted by the STM.

While the data fits well with the STM accounts illustrated in figure 4.7, some concerns are worth mentioning. First, the data do not cover the whole color spectrum. The results are restricted to one region of the color space where red, blue, and magenta are located, and the variations of the distractor color relative to the target were only in one direction (counterclockwise). Thus, it is needed to test a full range of colors to establish that attentional tuning works as a general mechanism in the color selection domain.

5.2.2 Attenuation of the N1 does not reflect distractor suppression.

In discussing experiment one, we asked whether the attenuation of the first GCBA response reflects a distractor suppression process (Gaspelin & Luck, 2018). The probe matching the target color might be a distractor because it contains the relevant color, potentially interfering with the current task in the focus of attention. It would be more critical (interfering) in the continuous condition than the onset condition, which would account for the attenuation to appear in the former, but not the latter condition. The attenuation may be a consequence of overlap from the Pd response elicited in the continuous condition contralateral to the probe. The experimental design here allowed comparing the GCBA response between two conditions of T-D similarity when the stimulus presentation mode was onset trial-by-trial. Attenuation of the response also in the high-T-D similarity condition speaks against the possibility that attenuation of the GCBA reflected a mere suppression of the probe response in experiment 1.

5.2.3.Color target selection based on the off-target gain as an alternative to on-target selective tuning.

Some studies have shown that the gain enhancement to discriminate the target features in small T-D distances is benefited when it is based on a gain enhancement of neighboring feature values (Hol & Treue, 2001; Scolari et al., 2012), i.e., in an overlapping region of tuning curves where more information for separating T and D values can be extracted. The reduced N1 response for the small T-D distance in the present experiment may be relative to a more remote enhancement seen for the off-target target-color matching probes. However, this possibility is unlikely as it implies that the control colors would be among the colors showing an off-target enhancement. Verifying such an alternative requires testing the probe response to gradually increasing T-D color distances. See chapter Perspective & Future research for a possible experimental approach.

5.2.4 Enhanced amplitude of the N2 response reflects color selection under conditions of high-task demands.

Previous studies have described a second modulation of the GCBA response called "discrimination matching" (Bartsch et al., 2015; Bondarenko et al., 2012): Discrimination matching reflects the discrimination of the color presented in the focus of attention. In the present data, the second modulation around ~ 260ms was larger in the high T-D versus the low-T-D similarity condition. This larger response has been previously observed in monkey cell-firing responses for hard versus easy discrimination tasks (Boudreau et al., 2006; Spitzer et al., 1988). In line with these findings, in human studies, similar enhancement of the global feature response to hard relative to easy discrimination tasks has also observed (Bartsch et al., 2018; Garcia-Lazaro et al., 2018).

5.3 Experiment 3

Experiment 3 focused on the question of whether the global color response elicited by reward-related colors (global reward-based selection, GRBS) could be dissociated from the global color response to target colors (GCBA). From previous work (Hopf et al., 2015), it is known that GRBS and GCBA are similar in terms of the time course, source localization (extra-striate visual areas), and amplitude. However, to what extent both GCBA and GRBS could be dissociated is unknown yet.

In experiment three, the unattended probe paradigm (Hopf et al., 2015) was used to test whether independence between both GCBA and GRBS responses exists. The experimental approach was to selectively manipulate factors known to influence attentional selection processes (attentional task load), but not reward-related factors. Specifically, the difficulty of target discrimination was varied while maintaining the reward-settings fixed. If target relevance and reward relevance were independent top-down modulatory effects, the manipulation in the target-color would exclusively affect the GCBA response associated to the target but not the GRBS response. Alternatively, if both GCBA and GRBS were not independently modulated at the top-down level, the manipulation of the attention load would affect both GCBA and GRBS responses.

5.3.1 GCBA and GRBS dissociate at the top-down level.

The data from experiment three showed that when manipulating the task-load settings while keeping reward-settings fixed, the target-probe response varied as a function of task-difficulty (easy vs. hard) but not the response for the reward-probes, control probes or target_reward probes. These results suggest that the manipulation of the attentional load was very selective for the target color. The amplitude increase of the GCBA for hard trials relative to easy occurred during the time of ~193-396ms, while the global reward-based response elicited from the extrastriate visual cortical areas does not differ as a function of task difficulty. Both GCBA and GRBS responses are in line with what has been observed previously in easy conditions (Hopf et al., 2015).

As expected, task-accuracy was higher in easy than in hard trials, but interestingly, response accuracy was facilitated when probing the reward-color in the hard condition. These findings are relevant because they support a mechanism of global color selection rather than attentional capture (Anderson et al., 2011; Folk & Remington, 1998), where the probe might be considered as a potential distractor capturing attention and disrupting the performance. Here, in contrast, task performance was higher when the probe contained the reward color relative to the other probe-conditions in hard trials.

While there was a selective increment of T-probes, no such enhancement was seen for the TR-probes of the hard condition. It is unclear why the task-load manipulation would only affect the target color when it is probed alone and not when the target- and reward-color are presented together. Unfortunately, the current data cannot exhaustively solve this question. In the following paragraphs, some alternative interpretations are discussed.

5.3.1.1 The T response is already at the ceiling on hard trials.

One possibility is that T-response in the hard condition reached a ceiling point such that adding the reward color did not allow for a further increment. This notion implies that such a ceiling point in the neural response exists, which cannot be verified with the current data. It would require testing point-

to-point the increments in the neural response as a function of increments in task-load. In the first part of experiment 3, such a procedure was used to determine the thresholds for task load.

5.3.1.2 TR color combination was coded as the "true reward" instead of R-color alone.

Another alternative interpretation is that the single reward-color (R) did not signal the reward, but instead, the combination of target and reward (TR) did. Subjects might have to build a template for TR combined instead of R alone; because subjects on rewarded trials the target and reward colors were combined in the attended stimulus. If this hypothesis were correct, no change in the TR response would have been expected between easy and hard conditions, since reward settings were kept constant over the experiment. Furthermore, data from this experiment can rule out a strict version of this possibility. In a strict sense, the response to reward-probes [R-probes] in both easy and hard conditions should not be enhanced relative to control-probes, given that the reward color on its own did not signal reward. Nevertheless, the data in Figures 4.14 and 4.15 showed that response to reward-probes increased significantly relative to control probes in both experimental conditions, easy and hard.

5.4 Experiment 4

Experiment four investigated whether previously attended colors, and previously reward-related colors elicit a global based response as current attended, and reward-related colors do. Previous empirical data have documented that intertrial repetition of target features facilitates their selection by speeding their responses (RTs) (Becker, 2008; Becker et al., 2014; Bichot & Schall, 1999, 2002; Goolsby et al., 2001; Hickey, Olivers et al., 2011; Maljkovic & Nakayama, 1994, 1996). This facilitation was associated with amplitude variations of the P1 (Hickey et al., 2011; Olivers & Hickey, 2010) and the N2pc component (Eimer et al., 2010; Hickey et al., 2011; Olivers & Hickey, 2010; Töllner et al., 2008). However, the experimental intention here was not to analyze the response elicited by repeated target colors as previous studies have done. Instead, this experiment focuses on testing the response driven by past relevant but currently irrelevant colors in trials when they were presented outside of the focus of attention (probes).

5.4.1 Response to target probes

The data from this experiment show that primed color probes elicit a significant enhancement of the early response relative to unprimed control colors. This early response modulation was similar to primed targets and target probes. In contrast, a late response modulation (arising roughly at ~ 200ms) only appeared to target probes, consistent with the well-known GFBA modulations elicited by attended colors.

The early response, therefore, is in line with a modulation of the feedforward sweep of information to all relevant features. It indexes feature relevance in a general manner at the perceptual level. However, the early response is not a task-defined top-down driven modulation since it does not differentiate between previous and current task-demands. It was confirmed by comparing the target probes response relative to primed targets (T-pT, see figure 4.21c). The actual enhancement in the response was observed when comparing primed target or target colors relative to control colors.

Moreover, the observation of an early latency response to targets here is in line with similar early feature-based responses seen by other groups (Moher et al., 2014; Zhang & Luck, 2009). Those have reported modulations of the P1 component consistent with a modulation of the initial stimulus-elicited feedforward sweep of processing in the visual cortex. Zhang & Luck (2009) observed the P1 modulation only when a competing distractor color was present in the attended field, suggested that the early P1 response reflects a selection process that biases the target color to resolve color competition. Moher at al., (2014) extended this research is showing that the P1 modulation may reflect the inhibition of the distractor color rather than the enhancement of the attended color. Based on the current data, it appears that the early response is an enhancement of the relevant colors (primed and target) relative to the control colors, which would only partially agree with Zhang & Luck (2009). The comparability between experiments is, of course, limited, as Zhang & Luck did not have an unbiased control color, and they never directly measured the effect of primed colors. Data from the present experiment suggest that the early effect in the P1 range reflects an enhancement of the relevant color because the control colors were truly neutral, i.e., they never served as target or reward color. Moher et al., (2004) included such a truly neutral color, but in contrast to the present experiment - they did not find a difference between target and neutral color. Instead, the P1 effect was a relative attenuation of the P1 response to the distractor color relative to the target color, which was taken to suggest that the early P1 modulation is in fact, suppression of the distractor color. Here, we did not test the probe response to a distractor color when paired with the target color in the focus of attention. Furthermore, Moher et al., (2014) kept the color assigned as the target, distractor, and control color unchanged throughout the experiment (within-subjects). These differences in experimental design make it difficult to compare data from the present experiment with those of Moher et al., (2014). Nevertheless, given the fixed color assignment in Moher et al., (2014), it is likely that consistent distractor attenuation was an effective strategy in Moher et al., (2014) but not in Zhang & Luck (2009). Such a strategy would also not be effective in the present experiment, which could at least partially explain why the control conditions are not comparable between studies. Overall, based on the current data, the possibility that in addition to the enhancement of the relevant colors, a suppression effect also contributes to the early P1 modulation cannot be ruled out.

It is worth mentioning that in Moher et al., (2014), the early response was followed by a late response modulation. The paper did not elaborate much on it. Because of the present data, the early response likely reflects a first filter based solely on feature relevance. The actual color selection and discrimination processes modulated by task demands occur later (top-down driven process), which would correspond with the late GFBA responses seen here.

5.4.2 Response to reward probes

Primed reward colors elicited an enhanced early response relative to unprimed colors arising from visual areas. This response appeared only to primed reward colors. The second response modulation appearing roughly at ~94ms prolonged to ~130ms was similar between current reward and primed reward colors. As for target probes (current and primed), the second response elicited by current and past reward seems to reflect general feature relevance.

The first early primed reward color might be more related to a conflict situation. Here, the primed reward color still carried over the relevance at a perceptual level because of signaling reward before, but at the same time, it is conflicting with the actual reward settings (Bush et al., 2002). This initial response to primed reward probes has not been seen before in our previous studies focused on GRBS

using the same unattended probe-paradigm (Hopf et al., 2015; Garcia-Lazaro et al., 2018), likely because of two main differences in the experimental designs. Here, the primed reward response was isolated from the response to the current reward-associations, and both were compared relative to control colors. In previous studies, in contrast, the control colors, due to counterbalancing, are the primed colors of earlier blocks. Thus, these earlier effects might be canceled out there.
Second, the task used here was a target detection task where subjects had to indicate the presence or absence of the target color, while in previous studies, the tasks used were discrimination tasks. This difference in task requirements might lead to different states in the color priority map and the readiness to elicit such earlier responses.

5.4.3 Coding of reward-related colors bias in visual cortices

The fact that reward modulations in experiment three and four were elicited independently of task-settings defining the target raises the question about how reward features are coded in the visual cortex. It is known from the literature that the perceptual representation of features-related to reward is enhanced (Serences, 2008), but where it differs from task-related features is not fully understood yet. The data from experiment three and four shows that target and reward responses are very similar in visual cortices. Therefore, it is likely that both attention and reward signals do not differ at this level of cortical representation. The dissociation instead appears outside of visual cortical regions. One possibility is that top-down signals dissociate in regions separately mediating the control of attention and reward such as anterior insula region, IPS, striatum, aMCC, caudate nucleus, Sustantia Nigra and Ventral Tegmental Area as previously reported (Boehler, Hopf, et al., 2011; Engelmann, 2009; Krebs, Boehler, Roberts, Song, & Woldorff, 2012). Alternatively, both target and reward signals might separate in structures related to attentional control like those belonging to the frontoparietal network (ACC, DLPFC, and Frontal eye fields) (Corbetta & Shulman, 2002; Kaping, Vinck, Hutchison, Everling, & Womelsdorf, 2011). These structures have a significant density of dopaminergic receptors (Noudoost, Chang, Steinmetz, & Moore, 2010; Noudoost & Moore, 2011), which potentially integrating independent contributions due to attention and reward, which are then combined to modulate visual cortex activity jointly.

6. Perspectives and Future Research

6.1 Selective tuning or gain enhancement of the off-target signals

The data presented in this work have contributed to answering open questions about the neural mechanisms of global feature-based selection and global reward-based selection. Nevertheless, as in any empirical work, open questions remain, and new questions arise. The following paragraphs propose experimental approaches to address two of these open questions.

In experiment one and two, an attenuation of the N1 response was observed. This reduction of amplitude was interpreted in terms of surrounding attenuation via selective tuning (STM). The selective tuning model proposes that units less optimally tuned to the target color (close neighbor of target) are pruned away. This inhibition leads to a reduction of the population response reflected in the smaller amplitude of components of the MEG response. Such attenuation (N1) was indeed observed for the target colors in experiments one and two. While this observation seems best accounted for by selective tuning, the data of experiment 1 & 2 do not provide a definitive interpretation. For the latter, it would be critical to show attenuation in the immediate vicinity of the target color. One approach to test GFBA in the surround of the target color would be to increase the probe-color distance to the target gradually. Besides, this would also allow addressing another alternative possibility, namely that the attentional gain enhancement to discriminate the target color is shifted away to neighboring colors (Hol & Treue, 2001; Scolari et al., 2012). That is, to increase color selectivity, the gain of units tuned slightly off-target could be enhanced, as this would better exploit the overlap-range of the target and the distractor color, where tuning differences are at a maximum. Thus, testing the response in those off-tune ranges is something that could reveal important further information.

The proposed experimental design consists of using the same unattended probe paradigm, while systematically varying the T-D color distances in the focus of attention and the probe color values. Figure 6.1 illustrates in a) the color values that stimuli will take in the attended location and probe. The chart shows an example of the red target, but the experiment would include three target colors: red, blue, and green. The distance between the target and distractor (T-D) will vary as in experiment 2. The probe will take different color values, going from close to further away to target color. This design will allow assessing the amplitude of the probe response as a function of color distance to the target (e.g., on target, off1, off2, off3), while subjects perform a color discrimination task varying in difficulty.

Figure 6.1b and 6.1.c illustrate two possible neural operations that could increase color selectivity. The first describes surround attenuation (figure 6.1.b). The second (figure 6.1c) illustrates off-target enhancement.

1) If color selection, under high T-D similarity conditions, were based on selective tuning, as proposed in this work, the expected probe-response would show a surround attenuation (SA) profile as the STM suggests (Tsotsos, 2011; Tsotsos et al., 1995). The SA-profile describes a zone of neural attenuation in the immediate surroundings of the target. Thus, the expected response would be a response enhancement when the color-value is on-target, relative to suppression when it is off-target but next to the target. It would recover for off-target color-values further away from the target (see figure 6.2.b).
2) Color selection under high T-D similarity conditions may instead be based on increasing the gain of neighboring colors farther away from the target and the distractor, where the latter elicit responses with a bigger difference than at the target or the distractor color. That is the response difference between the target ad the distractor color be smaller on-target relative to

off-target. A GCBA enhancement at an appropriate off-target color would gain more response differences than at the target color itself (Hol & Treue, 2001; Scolari et al., 2012).

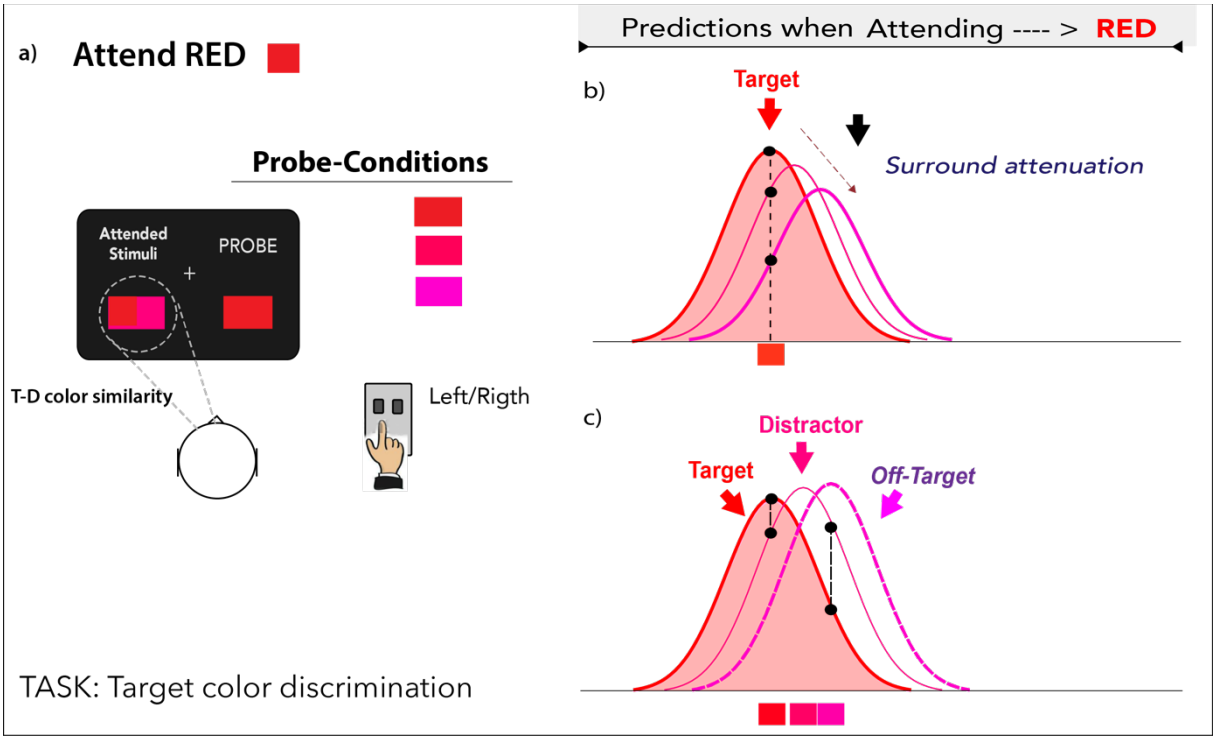

Figure 6.1 A illustrates T-D color distance in the attended stimuli and the color values that the probe will take. B and C show two alternative mechanisms for color selectivity. B describes the surrounding attenuation vía selective tuning (STM). C shows that gain enhancement of the off-target signals maximizes the discrimination between the target and distractor.

6.2 Task-load as an account of the attenuation of the N1

The attenuation of the N1 response observed in experiments one and two were interpreted in terms of surround attenuation vía selective tuning (STM). Such attenuation is thought to reflect the inhibition of the nearby to target neuronal signals not tuned to the target color. While STM fits well with our findings, it remains open whether the pure task load differences between the low versus high T-D color similarity might explain such response attenuation. To rule out this possibility, one could compare the GCBA while varying the task difficulty independent of the difficulty of color discrimination in the focus of attention. One way to do this is to manipulate task difficulty based on a feature that is orthogonal to color. In the following proposed experimental design, color and grating orientation will be used as features. The difficulty of discriminating grating orientation will vary: easy and hard, while the color will define the target and probe conditions.

Figure 6.2 shows the proposed experimental design. Color changes in the target and probe stimulus. Two main probe conditions will be derived: the probe matches the attended color versus it does not match the target color (Match versus non-match). Figure 6.2.b shows orientation manipulation of the attended stimuli. The task consists of indicating whether the grating orientation of the target is tilt to the left or the right. The larger the distance of the gratings from the vertical [0°], the easier the task will

be. Two levels of difficulty will be defined individually to set similar levels of task performance across subjects, while the same color settings will be used for easy and hard conditions.

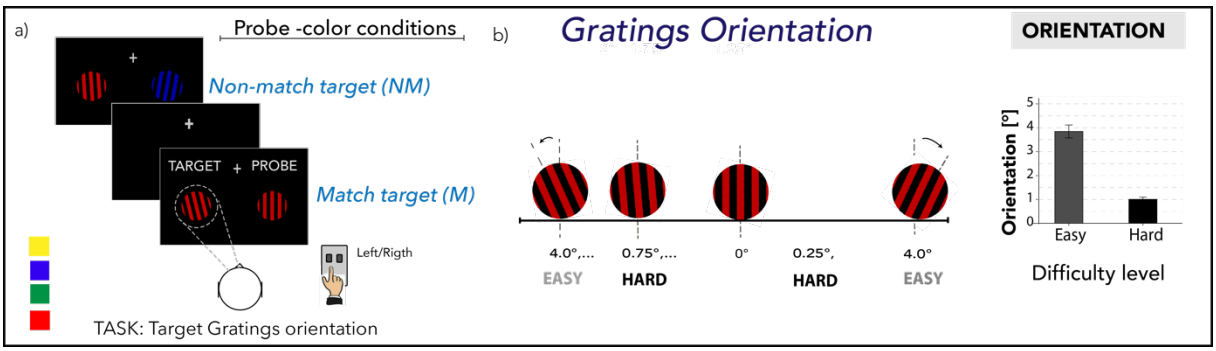

Figure 6.2 shows the experimental design varying color and orientation of stimuli. Task's subjects consist of discriminate against the orientation of the target (Tilt to the left or the right). B shows the gratings orientation variation in the focus of attention for two levels of difficulty: easy and hard. B shows the color variation in the target and probe stimulus.

The prediction would be that if task load per se accounted for the amplitude reduction of the N1 wave in experiments 1 and 2, it should also appear under the here proposed experimental manipulation of task difficulty.

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