Reward- and Attention-Related Determinants of Color Selection in Human Visual Cortex

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Zusammenfassung

Belohnung ist eine der größten Einflussgrößen für Verhalten bei Tieren und Menschen. Viele Publikationen haben bereits einen Einfluss von Belohnung auf die visuelle Wahrnehmung sogar auf frühen Stufen sensorischer Verarbeitung dokumentiert. Selektive Aufmerksamkeit versetzt Individuen in die Lage, wichtige Information aus einer Flut von visuellen Reizen zu extrahieren. Sie spielt insbesondere bei visueller Suche eine große Rolle, indem sie ermöglicht, Stimulus-Eigenschaften (Englisch “features”) des gesuchten Ziels bevorzugt zu verarbeiten. Diese bevorzugte Verarbeitung von attendierten Features schlägt sich in Amplitudenerhöhungen der neuromagnetischen Hirnaktivität nieder. Features, welche mit Belohnung assoziiert werden, scheinen eine ähnliche bevorzugte neuronale Verarbeitung hervorzurufen. Maunsell (2004) weist jedoch darauf hin, dass solche belohnungsspezifischen Effekte insbesondere in Tierversuchen nicht korrekt interpretiert worden sein könnten, da die experimentellen Bedingungen hier typischerweise keine Trennung von Belohnungsreiz und attendiertem Zielreiz zulassen (d.h. der attendierte Stimulus ist der, für den es auch die Belohnung gibt). Um die frühe visuelle Verarbeitung von belohnungs-assoziierten Features untersuchen zu können, wurden im Versuchsaufbau dieser Arbeit Ziel- und Belohnungsreiz operational getrennt. Menschliche Probanden suchten in einem visuellen Experiment auf der Basis einer definierten Farbe (Zielfarbe) nach einem zweifach kolorierten Zielobjekt. Belohnt wurde diese Suche, wenn das Suchziel die Zielfarbe in Kombination mit einer Belohnung-definierenden Farbe (Belohnungsfarbe) aufwies. Die Mehrheit der Durchgänge wurde jedoch nicht belohnt, und das Auftreten der Belohnungsfarbe in Distraktorobjekten war für die Aufgabe vollkommen irrelevant. In visuellen Suchexperimenten dieser Art entwickeln Probanden eine „Aufmerksamkeitsgrundeinstellung“ (attentional set) für die Aufgabe und die Farbeigenschaft.

Die Arbeit untersucht im Speziellen, ob und wie die Hirnantwort zu irrelevanten Farbstimuli (Distraktoren) von der Farbrelevanz (aufmerksamkeits-, belohnungs-relevant, komplett irrelevant) abhängt. Die Prädiktionen der Arbeit orientieren sich an der einflussreichen Theorie der kontingenten attentionalen Orientierung (contingent involuntary orienting, siehe Folk et al., 1992), welche postuliert, dass ein Distraktor unwillentlich mehr Aufmerksamkeit auf sich zieht, wenn er Eigenschaften des Zielreizes teilt. In Experiment 1 und 2 wurden aufmersamkeitsanziehende Distraktoren (hier „Probes“ genannt) zwischen den Suchaufgaben präsentiert, d.h. zu einem komplett aufgabenirrelevanten Zeitpunkt der Experimente. Die von der “Zielfarbe” ausgelöste Aufmerksamkeitsorientierung war in den Experimenten dieser Arbeit eindeutig nachzuweisen. D.h. zwischen 180 und 280 ms nach der Präsentation des Probes löste die Zielfarbe des Zielreizes im Vergleich zur “Referenzfarbe” eine erhöhte elektromagnetische Aktivierung im ventralen extrastriären Kortex aus. Für die Belohnungsfarbe wurde solch eine Aktivierung nicht gefunden. Selbst nach Erhöhung der Belohnung auf das Doppelte (10 Cent) im zweiten Experiment, war keine bevorzugte Verarbeitung der Probes nachzuweisen. Allerdings kam es hier zu einer verminderten extrastriären Antwort zwischen 220 und 250 ms. Interessanterweise zeigte sich, dass der Grad der Verminderung der extrastriären Antwort mit der zuvor (160-180 ms) erhöhten Aktivität im dorsalen anterioren cingulären Kortex (dACC) korrelierte. Letztere Beobachtung spricht dabei für eine aktive Suppression der belohnungs-abhängigen Farbantwort im extrastriären Kortex, die unter strategischer Kontrolle von dorsomedialen frontalen Hirnstrukturen erfolgt.

Eine ähnliche strategische Suppression der belohnungsabhängigen extrastriären Antwort zeigte sich bei der Analyse der Hirnantwort, die während Diskrimination des Suchzieles ausgelöst wurde. Bei moderater Belohnungshöhe lösten Distraktoren mit der Belohnungsfarbe, eine erhöhte Antwort im kontralateralen extrastriären Kortex aus. Unter Bedingungen von erhöhter Belohnungserwartung (Experiment 2) war die gesteigerte Antwort jedoch nicht mehr nachzuweisen.

Experiment 3 erlaubte mit einem modifizierten Paradigma (fixer Fokus der Aufmerksamkeit) die Analyse der Hirnantwort von Distraktoren mit der Ziel- oder Belohnungsfarbe, sowie deren Kombination während Diskrimination des Suchzieles. Unter diesen Bedingungen lösten Ziel- und Belohnungsfarbe ähnliche Antworten in überlappenden extrastriären Arealen aus, wobei die Amplitude der Antworten additiv war. D.h. die Höhe der Antwort auf die kombinierte Präsentation der Ziel- und Belohnungsfarbe glich nahezu perfekt der Summe der separaten Antworten auf die Ziel- und Belohnungsfarbe.

Zusammenfassend lässt sich sagen, dass sich Belohnung und Aufmerksamkeit beide durch denselben Mechanismus visueller Selektion im visuellen Kortex zu manifestieren scheinen, wohingegen dieser jedoch von hierarchisch höher gelegenen (frontalen) Hirnarealen durch Belohnung und Aufmerksamkeit unabhängig moduliert wird. So können belohnungsbezogene Merkmale im Sinne effektiver Verhaltensadaptation unterdrückt werden, während gleichzeitig die Repräsentation aufgaben-relevanter Merkmale gesteigert wird.

Summary

Reward is a major driving force of human behavior. So far, however, there have been only a few attempts to investigate the influence of reward on perception at elementary levels of feature processing. In particular the question whether reward-based modulations represent an effect that is independent of the effects of attention, or whether both refer to the same modulation is currently debated (cf. Maunsell, 2004). To address this issue effectively, it is important to avoid confounding top-down settings defining task-relevance with those defining reward-relevance. In the experiments reported here we aimed at a dissociation of the target's definition (attention to color) from reward-relevance (color associated with reward).

To analyze the effect of reward and attention I compared the neuromagnetic brain responses to task-irrelevant color probes drawn in the target- and reward-color. I observed an enhanced activity between 180 and 280 ms in ventral extrastriate cortex for the target but not for the reward-color (Experiment 1). Doubling the reward prospect (Experiment 2) caused a response-attenuation for the reward-color (220-250 ms). Notably, the degree of attenuation was found to correlate with the latency of a prior activity enhancement (160-180 ms) in dorsal anterior cingulate cortex, suggesting that the neural attenuation of the reward-color reflects active top-down suppression. A further analysis of the response to task-relevant search arrays supports this interpretation. The reward-color presented in search distractors produced a relative response enhancement in Experiment 1, but this was eliminated when doubling the reward prospect in Experiment 2.

A third experiment aimed at analyzing the response enhancement under moderate reward expectations in more detail. Here a modified experimental setup was used to allow for a direct comparison of the brain response to the reward- and target-color outside the focus of attention. We observed comparable modulations in overlapping areas of the ventral extrastriate cortex. The response to the reward-color was delayed but otherwise roughly identical to the early modulation underlying target feature selection. The latter effect has been shown to reflect the feature template-matching phase of global feature-based attention (Bartsch et al. 2014). Importantly, independent of their relative time-course, the modulations to the target- and reward-color added up to match the response size of their combined presentation.

The present results suggest that reward and attention recruit the same visual global feature selection mechanisms in extrastriate cortex, but that they are under top-down control from independent sources. The brain may not be able to entirely "ignore" reward information but it may be effective in eliminating its distracting effect via top-down suppression.

Table of Content

Acknowledgements

In 2006 I began to work in the Clinic for Neurology II in Magdeburg on my diploma thesis and my swimming skills were much more advanced than anything I knew in the field of neuroscience. Entering the words “attention” or “reward” (in the title) in PubMed disgorges over 30.000 scientific publications. In the past years I got a coarse overview over this expanding field of cognitive neuroscience and I am grateful to my supervisor Prof. Jens-Max Hopf to share some of his great knowledge with me. I would also like to say a big “thank you!” to Prof. Ariel Schoenfeld for the reliable support and for always listening to my problems.

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1 Introduction

1.1 Reward and Attention

In every moment that we are awake our eyes and brain are exposed to a sheer bombardment of sensory stimuli. But processing capacities are inherently limited, so that only a small amount of this visual input reaches conscious perception. Selective attention modulates ongoing processing of visual input by resolving competition between stimuli. Thereby especially behaviorally relevant stimuli gain access to perceptual awareness. The link between visual selective attention and goal-directed behavior is subject to this work.

Reward is beneath punishment the greatest driving force of goal-directed behavior. Already in the beginning of the twentieth century Thorndike (1911) used reward in animal experiments to study learning behavior. Within the scope of his learning theory he postulated the “law of effect” saying that a reaction, which is followed by a “satisfying state of affairs” (reward) will strengthen the association between these positive situation and the respective behavior. Thorndike´s work paved the way for behaviorism known for learning theories like operant conditioning (Skinner, 1938). In contrast to classical pavlovian conditioning, explaining behavior on a reflex-like stimulus-response basis, operant conditioning links normal behavior (of animals) to reward. Here, reward is used to reinforce learning (positive reinforcer) leading to increased frequency and intensity of behavior needed for the acquisition of goal objects. Also volitional goal-directed behavior requires the detection of reward information. For their decision behavior animals and humans consciously or unconsciously evaluate benefits and costs associated with attaining primary rewards (like food) or secondary rewarding objects (like money in humans). (Schultz, 2000) Or as Gottlieb (2012) put it recently, the brain has not just the highly complex task to analyze visual input, but also to “determine the significance and value of that information”.

But Reinforcement[1] and punishment are not only registered and linked to certain stimuli to affect behavior, but might but also influence sensory processing itself, i.e. reward could have the capability to alter perception for instance via attentional modulations.

At this point it might be reasonable to elaborate on attention in general to avoid verbal confusion. The term attention refers to many different meanings in everyday language. These involve consciousness, awareness, alerting and attentiveness. For example, alertness overlaps with notions like sustained attention and vigilance and all can be defined as “the ability to increase and maintain response readiness in preparation for an impending stimulus” (Raz and Buhle, 2006). Sturm (2005) developed a taxonomic table for attention based on neurological dysfunctions and common clinical paradigms that test for attention. He splits attention into two categories: The intensity dimension of attention - including alertness, sustained attention and vigilance - comes close to the non-scientific understanding of attention and concerns changes in global state or arousal of an animal or human being. The second is the selective dimension of attention comprising selective and divided attention. In the work presented here the word “attention” always refers to the selective aspect of sensory processing of visual stimuli.

Pashler (1998) annotates that “Folk psychology postulates a kind of substance or process (attention) that can be devoted (paid) to stimuli or withheld from them. Whether or not attention is allocated to a stimulus is usually thought to depend on a voluntary act of will (…). Sometimes however, attention is directed or grabbed without any voluntary choice having taken place, even against strong wishes to the contrary; this is the phenomenon of distraction.” The phenomenon of distraction described by Pashler bases on stimulus-driven or bottom-up visual selection. Considerable experimental evidence suggests that the sudden onset of an unexpected visual stimulus can draw attention in an automatic fashion - an effect referred to as attentional capture (Yantis, 1996, 1998, Theeuwes, 2010). In other words, the features of an item and in particular its feature contrast with other items in a scene, makes the item standing out and therefore capture visual attention.

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[1] The term “reinforcement” in the behaviorist sense means strengthening of a habit, but here reinforcement is extended to describe the reward-related increase of a neural response (for a discussion see Berridge and Robinson, 1998).

Such an attention-capturing item is called to be salient. But behavior is not just stimulus driven but also controlled by personal goals and will. Voluntary control of attention acts “top-down” on selection of visual stimuli (Corbetta and Shulman, 2002). Most behavior seems to lie between the two extremes of responding in a reflexive way to a stimulus or being guided by goal-directed behavior. The distinction of top-down and bottom-up control of attention is not absolute. Bottom-up attention caused by salient items can be influenced involuntary by top-down processes. For example, orienting towards a salient item in visual search is stronger if one feature of this item (color, form or orientation), matches the features of the target. Looking for a person wearing a red hat causes a red scarf of another person to catch my attention. This would be not the case, if I searched for a person with a green hat. The red scarf shares the feature color with the target and therefore catches attention in a bottom-up way, but contingent on the goal of the search (contingent involuntary orienting theory by Folk et al., 1992). Provided that subjects of a visual search experiment (such as the search for hat-shaped objects in red) are instructed well, they will develop an executive task set (Dosenbach et al., 2006) to perform the task and therefore enable attentional capture contingent on high-level goals.

The association of reward with visual features might lead to biasing of sensory selection in extrastriate cortex analogue to task-relevant features. And if so, the question remains if reward processing is a class of its own or resembles the selection operation seen for attentional selection. (Buschschulte et al., 2014, Hopf et al., 2015)

1.2 Functional Anatomy of the Visual System

The visual system is the part of the central nervous system, which enables organisms to interpret information from visible light to build a representation of the surrounding environment. Vision is the highest developed sense in primates and also the best studied.

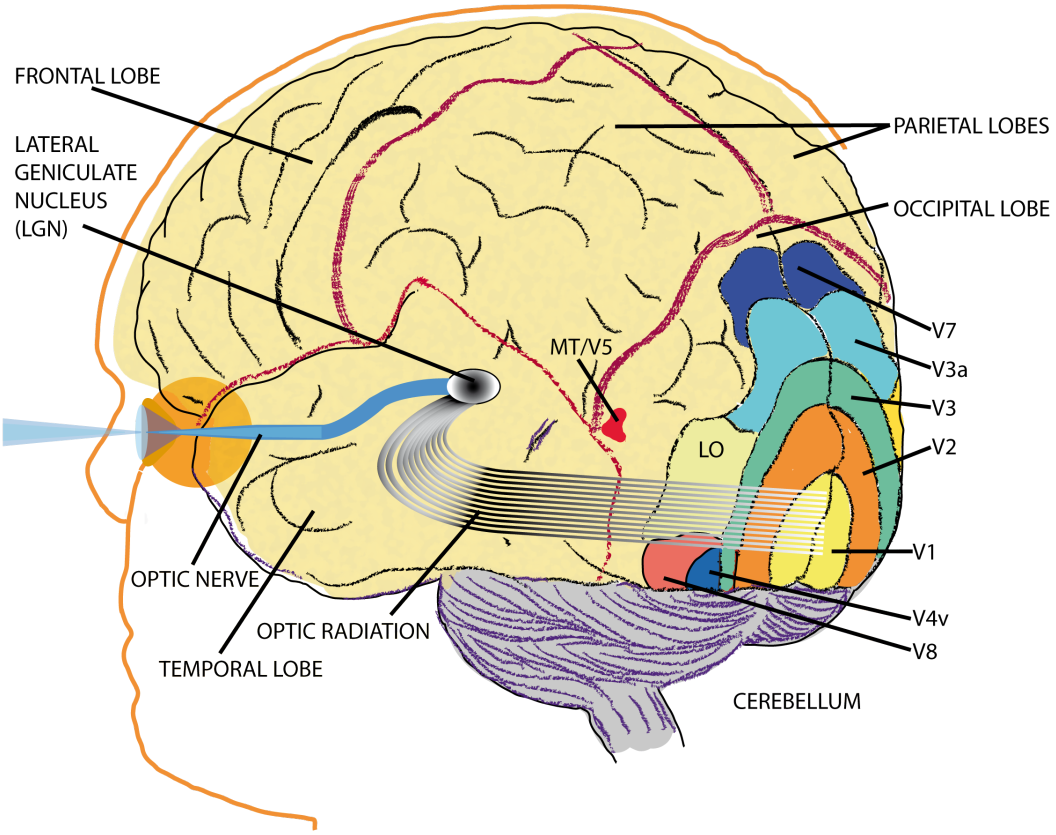

Figure 1: The visual system. Shown are eye, optic nerve, lateral geniculate nucleus (LGN), optic radiation and visual cortical areas in different colors. With exception of the middle temporal (MT) and lateral occipital area (LO) all visual areas begin with V for visual and are consecutively numbered from 1 to 8 (a = anterior, v = ventral). The borders of the brain lobes (frontal, parietal, temporal, occipital) are marked with red lines (modified according to a picture originating from a Stanford University lecture 2009 (www.brain-maps.com)).

About 50% of cerebral cortex in macaque monkeys and 20–30% in humans is devoted to vision. The auditory cortex for example makes up only 3% of the cerebral cortex in monkeys and 8% in humans. (Orban et al., 2004) Contrary to introspection the visual system does not gain information about a complex visual scene in an automatic way like a camera. The transformation of light information into a coherent internal representation of the environment is by no means simple.
In the retina of the eye photoreceptors (rods and cones) convert information of light into membrane potentials, which are then transformed into action potentials for further processing in sensory neurons. All sensory neurons, for example ganglion cells or neurons in visual cortex, have receptive fields (RF), describing the region of space in which the presence of a stimulus will alter the firing of the neuron. A cortex neuron with a big RF processes information from many ganglion cells and photoreceptors. As illustrated in Figure 1 about 90% of all axons of the optical nerve project to the lateral geniculate nucleus (LGN) of the thalamus and further on via the optic radiation (radiatio optica) to the primary visual cortex (V1). Another name for V1 is “striate cortex”, and all other visual areas subsume under “extrastriate cortex” respectively. The remaining 10% of the optical fibers innervate subcortical structures like the pulvinar nucleus of the thalamus and the superior colliculus (SC) of the midbrain. The optic nerves from both eyes meet and cross before LGN at the optic chiasm (not shown in Figure 1). At this point the information coming from both eyes is combined and then splits according to the visual field (VF). The corresponding halves of the field of view (right and left) project to the left and right halves of the brain. So the right side of primary visual cortex (V1) gets information from the left half of the field of view from both eyes and vice versa. Beyond area V1 visual information is conveyed to a huge number of extrastriate areas (see Figure 1), which exhibit a hierarchical order (Felleman and Van Essen, 1991).

Despite the complexity of interconnections between these different areas, two general “streams” have been identified in the macaque monkey brain as illustrated schematically in Figure 2. Both streams proceed together from V1 via extrastriate areas V2 to V3 and then split into a ventral, or occipitotemporal pathway and a dorsal, or occipitoparietal pathway. (Ungerleider and Mishkin, 1982, Goodale and Milner, 1992)

The ventral stream continues via V4, TEO, and TE and leads to the inferior temporal cortex (IT), which is believed to be the last area in the processing hierarchy that is feature selective (cf. Baluch and Itti, 2011). Functionally this stream is sometimes called "what-pathway", because it is specialized for object recognition and perception. For instance, V4 is one of the best-studied areas within the ventral stream. V4 neurons are selective for color, orientation, disparity (Hinkle and Connor, 2001, Watanabe et al., 2002), as well as 3D contour (Hinkle and Connor, 2002) and can be localized in the area of fusiform and lingual gyrus and the collateral sulcus (Desimone and Schein, 1987, Schein and Desimone, 1990, McKeefry and Zeki, 1997). The Outputs of V4 provide the principal visual inputs to the highly complex neurons in the inferotemporal areas TEO and TE.

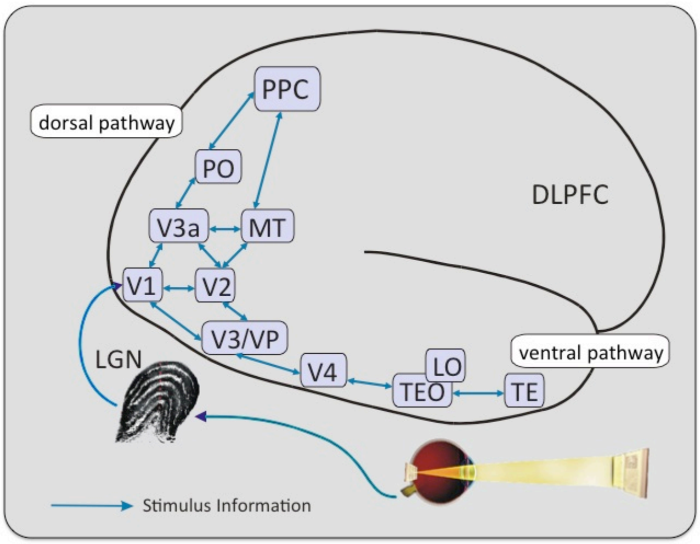

Figure 2: General scheme showing dorsal and ventral stream in visual information processing. Visual areas are schematically depicted in boxes. The way and direction of visual information beginning in the retina of the eye, continuing via visual areas in hierarchical order is shown in blue arrows. Information of the ventral stream, also called „what-pathway", is conveyed from V1 over V2, the ventral part of the third visual areaV3/VP, and V4 to temporo-occipital cortex (TEO), lateral occipital cortex (LO) and the inferior temporal cortex (TE). Analogue the dorsal stream or „where-pathway" starts in V1/V2 and continues over V3a to parieto-occipital (PO), middle temporal (MT) and posterior parietal cortex (PPC). For orientation also the dorsolateral prefrontal cortex is labeled. (with courtesy of Steven Hillyard (modified), 2011)

The dorsal stream continues via V3a to posterior parietal regions and is also called "where-pathway". Spatial perception such as the sense of depth, object location, as well as object relations in space are functions of this pathway. Here V5/MT (middle temporal area) is the best investigated area involved in motion processing, which lies at the junction of parietal, temporal and occipital cortex (Zeki et al., 1991, Tootell et al., 1995). Although one has to be cautious to generalize from monkey to human, neuroimaging evidence suggests, that the dissociation in ventral and dorsal stream is also present in humans (Haxby et al., 1991, Culham and Kanwisher, 2001, Tootell et al., 2003). The visual cortex represents the visual scene retinotopically. That is, nearby locations in environment are represented nearby in visual areas V1 to V8. Receptive field (RF) sizes increase from V1 to higher areas, so that the complexity of stimulus representation increases. That is, for instance V1-Neurons with their small RFs code fine spatial and featural details, while neurons in later areas have large RFs and code more complex visual aspects such as whole objects.

This is meaningful for attentional selection. To be able to recognize or locate objects unnecessary information has to be removed. Competitive selection separates the wheat from the chaff because stimuli compete for dominance in all hierarchy levels. A current model suggests that visual stimuli or their electrophysiological correlates compete in apriority map, a topographical 2D network where the activity of the cells in the map represents the priority or salience of a given spatial location (Koch and Ullman, 1985, Itti and Koch, 2000, 2001). Salient features of the visual environment are combined with top-down influences into a general measure of priority and represented by a "peak" on a spatial map. To resolve the competition between stimuli selective attention plays a major role. According to the model mentioned above, attentional selection occurs on the basis of a "winner-takes-it-all" and moment-to-moment competition between dynamically changing peaks on the priority map. Possible locations for the proposed priority map are lateral intraparietal cortex (LIP), frontal eye fields (FEF), and superior colliculus (SC) (Baluch and Itti, 2011).

Attentional modulations have been shown to occur in all visual areas and they follow the retinotopical organization of the visual system. (e.g. Tootell et al., 1998, Cook and Maunsell, 2002, Serences and Yantis, 2006)

1.3 Reference Frame of Selective Attention

Yantis (2003) says “to see is to attend”, because even masses of neurons are not able to process and analyze all visual inputs. Therefore as Knudsen (2007) puts it “to behave adaptively in a complex world, an animal must select, from a wealth of information available to it, the information that is most relevant at any point in time.” There were and still are many models and theories how, where and when visual attentional selection takes place. Theories in the 1950ies and 60ies proposed a filter mechanism, influencing either “early” or “late” stages of visual processing. That is, for “early” selection a stimulus does not have to be analyzed completely to be selected (or rejected), whereby “late” selection means that also ignored stimuli reach a stage of semantic analysis. (Gazzaniga, 2009)

In behavioral studies (which were apart from lesion-studies the only possible studies before advent of modern neuroimaging/electrophysiological techniques) the main difficulty is to determine the stage or neuroanatomical locus of selection, because behavior reflects the output of processing and does not directly reveal the individual steps that led to that output.

Broadbent (1958) proposed a filter theory based on “early selection” of physical stimulus properties. According to this theory, distracting stimuli would not reach higher processing stages. The early selection theory was expanded by Treisman (1964). She proposed that unattended information would not be completely filtered out, only attenuated (“attenuation theory”). Information could reach higher stages of analysis with greatly reduced signal strength. Her later “feature integration theory” assumes that features like color or orientation are coded automatically and in parallel without attention. To select objects, attention is needed to bind features for object - identification.

Late selection theories hypothesize that all stimuli are processed equivalently by the perceptual system and that selection takes place only at higher processing stages. Then the system “decides” whether stimuli should gain complete access to awareness or not. (Deutsch and Deutsch, 1963)

According to the late selection account every stimulus in the visual field is fully identified, but only attended stimuli are stored in working memory so that they can be reported or a response can be initiated. (Duncan and Humphreys, 1989, Duncan and Humphreys, 1992, Duncan et al., 1997)

Nowadays the discussion, were the processing bottleneck could be located, faded, because there is evidence for more than one attentional mechanism. Research in this expanding field made clear, “that multiple selection processes cooperate in a flexible manner to guarantee the adaptability of attention to a wide range of circumstances” (Hopf et al., 2009).

In the context of stimulus and task properties selective attention can be traditionally assigned to three different categories. Attention can refer to a location in the visual field (spatial attention), to a certain object (object-based attention) or to single features (feature based-attention) of one or more items in the visual field.

1.3.1 Spatial Selection

Spatial attention has been envisioned as a spotlight that illuminates a circumscribed region in the visual scene, and which can be directed to a location without moving the eyes (covert attentional orienting) (Helmholtz, 1909-1911). Within the spotlight information is processed faster and more efficient. This can be shown for example with the spatial-cuing task – a paradigm that has the following general design: While subjects focus the center of a screen they are asked to covertly attend to a target stimulus appearing at the right or left side of the screen. Before the target appears a central cue (e.g. arrow) is presented telling the subject the location (left/right) where the target will appear with a certain probability. If the target appears at the cued location the trial is said to be valid, otherwise it would be invalid (or neutral if the cue gives no information regarding the target´s location). Under typical circumstances subjects respond faster and more correctly on validly compared to invalidly cued trials. (Posner, 1980) Relative to a neutral condition a cue causes costs and benefits in performance. The cue itself is thought to attract spatial attention due to contingency on target features or simply because it has an abrupt onset (e.g. Sawaki and Luck, 2010) (for closer consideration see section 1.4 Contingent Attentional Capture).

1.3.1.1 Electrophysiological Evidence

Early evidence for spatial attention was provided by Goldberg and Wurtz (1972). Single cell recordings in neurons of the superior colliculi of rhesus monkeys performing a saccadic cuing-task showed that the neurons response was enhanced if the stimulus in its receptive field was the monkeys´ saccade target compared to an ignored stimulus.

Electroencephalography (EEG) is a powerful non-invasive method to visualize cortical brain activity in response to visual (and other) stimuli in humans. Under experimental conditions electrical potentials that correlate with the a repeated presentation of a visual stimulus - so called event related potentials (ERPs) - are averaged over many experimental trials and analyzed in regard to different experimental conditions. Visual selective attention has been demonstrated to be reflected by amplitude modulations of early-latency sensory ERP-components as shown schematically in Figure 3.

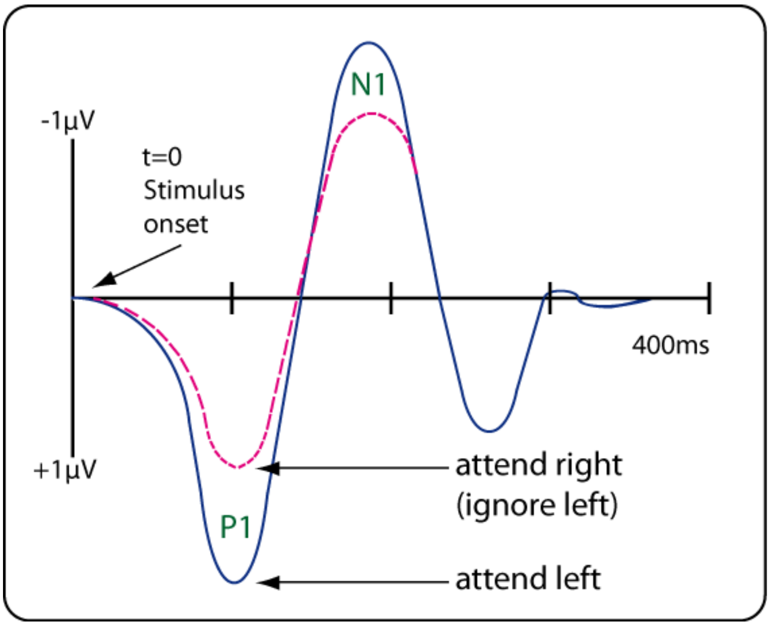

Figure 3: Example for visual cortical event-related potentials evoked by a left-field stimulus under an attended and a not attended condition. EEG-waveforms show a similar topography like the one drawn here and are typically recorded from an occipital electrode site contralateral to stimulus presentation. The components are named after their positive or negative deflection and their ordinal position (P1 = first positive deflection). Attended stimuli (blue trace) elicit ERPs with greater amplitude than unattended stimuli (dashed red trace) do. Note, in contrast to standard conventions negativity is plotted upwards here.

In particular the initial sensory components, the first positive (P1) and negative voltage (N1) show enhanced amplitudes when elicited by a stimulus at an attended versus an unattended location. The enlarged P1 (at 80 – 130 ms post stimulus) and N1 (at 130 – 200 ms) components are modulated in tandem for choice-reaction tasks and the modulation is strongest over the lateral occipital scalp contralateral to the VF of target presentation. The P1-deflection reflects a modulation of the attentional distribution in space per se and the subsequent N1-modulation reflects discriminative processing of the stimulus within the focus of attention (Mangun and Hillyard, 1991, reviewed in Hopf et al., 2009). Magnetoencephalography (MEG) can be used analogous to EEG (cf. Hopf et al., 2002b) and is explained in detail in section 3.1 “Magnetoencephalography Basics”.

Attention can be exogenously attracted to a location with a visual cue preceding the target stimulus. Is the interstimulus interval (ISI) short, meaning less than about 250 ms, response times are faster at cued than at uncued locations. Hopfinger and Mangun (1998, 2001) could demonstrate that ERPs for such reflexive cuing paradigms show an enlarged occipital P1-modulation for targets that quickly follow the cue. Both, reflexive (bottom-up) and voluntary (top-down) shifts in spatial attention induce similar electrophysiological modulations in early visual processing.

Notably, longer periods between cue and target reverse the effect and the P1-response is diminished or may be even inhibited. The latter effect presumably reflects a consequence of Inhibition of Return (IOR). IOR was originally discovered by Posner et al. (1984) and Berlucchi et al. 1987 (Lupianez et al., 2006) with reaction time measurements in human subjects (see Figure 4). As the name suggests the recently attended location becomes inhibited over time such that following responses to stimuli in that location are slowed. Posner and Cohen (1984) suggest “(…), that the inhibition effect evolved to maximize sampling of the visual environment.” and therefore encourages foraging towards novel and uninspected items (Klein and MacInnes, 1999, Wang and Klein, 2010). To prove the “foraging-hypothesis” Klein (1988) developed a “probe-following-search” paradigm, in which a visual search task serves as “cue”, while a probes presented at item locations following the search array serves to assess the IOR effect.

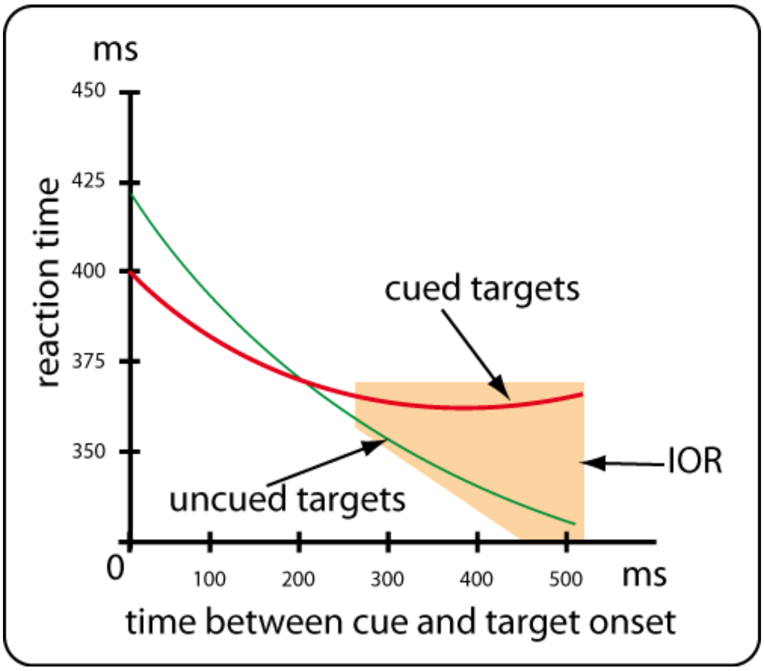

Figure 4: Idealized illustration of the Inhibition of Return-effect. The underlying simple cue-target experiment consists of two possible locations for cue and target beneath central fixation on the screen. Subjects have to make a speeded detection response to the target. Reaction times are plotted against the ISI between cue and target. A cued target (red curve) follows at the same position as the cue, an uncued target (green curve) at the position opposite to the cue´s position. Faster response times to cued targets at the shorter ISIs (till about 200 ms) reflect the facilitatory effect of reflexive orienting of attention toward the cue. IOR is reflected in the slower responding to targets at the cued location at longer ISIs (longer than 200 ms; orange box). (modified after Klein, 2000)

In difficult search tasks the inhibition can be object- or scene-based, so that when the scene is removed in most cases IOR effects are removed as well (Tipper et al., 1994, Wang and Klein, 2010). Nonetheless location-based components are involved in eliciting IOR (Muller and von Muhlenen, 2000, Leek et al., 2003). The time-course of IOR turns out to depend on experimental conditions. Inhibition begins earlier when saccadic responses are made as compared to when manual responses are required (Klein, 2000). Earliest crossover points, where facilitation changes into inhibition occur at 200 ms inter stimulus interval (ISI) between cue and target for a simple cue-target task (see Figure 4), whereas difficult discrimination tasks can show crossover latencies between 500 and 600 ms ISI. IOR can last for several seconds (Klein, 2000).

To anatomically localize the cortical areas that generate ERP- or analogue MEG-components, EEG-and MEG-recordings were combined with functional magnetic resonance imaging (fMRT) or positron emission tomography (PET). Generators of the P1-and N1-attention effect were found to originate in ventral extrastriate cortex. (Heinze et al., 1994, Di Russo et al., 2001, Martinez et al., 2001) Amplitude enhancements of the P1/N1 component typically occur without changes in component latencies or scalp topographies, which was taken to indicate that spatial attention selects visual input during early processing stages by exclusively controlling the gain of the cortical response to the input (Hillyard et al., 1998). Single-unit studies in the monkey support such a gain control mechanism (Luck et al., 1997, Maunsell and Cook, 2002, Lee et al., 2007).

The focus of attention can vary in form and size depending on task demands. Its form has been linked to a spotlight, a zoom lens (Eriksen and James, 1986), or a Gaussian gradient (Downing and Pinker, 1985). (cf. Hopf et al., 2009) It has been shown recently that the spatial distribution of attention can resemble a Mexican hat profile (Hopf et al., 2006). The processing of stimuli is most enhanced central, suppressed next to the center and then again progressively enhanced in the periphery.

1.3.2 Feature-based Selection

The ability to enhance the representation of image components throughout the visual field that are related to a particular feature is referred to as feature-based attention (FBA) or selection. FBA is particularly important in visual search. For example, identifying my red car on a crowded parking lot makes the color red an important feature for my search. Common to all visual search paradigms is the requirement to detect a target item (red car) among distractor items (cars in other colors) based on previously known feature descriptions with the target differing from distractors in at least one feature-dimension, such as color, form or orientation. As FBA enhances the representation of image components that match the attended feature (e.g. the color red or a vertical orientation) (e.g. Maunsell and Treue, 2006) search is biased towards target identification. Global feature-based attention is the phenomenon of FBA expanded to target-relevant features outside the focus of attention (Hopf et al., 2009).

1.3.2.1 Electrophysiological Evidence

The enhancement/decrement of a certain component of the visual scene corresponds physiologically with a modulation of cell firing rates in visual neurons. Such sensory gain control through attentional selection can operate by increasing the gain of neuronal representations that match the attended feature (Motter, 1994, Treue and Martinez Trujillo, 1999, Maunsell and Treue, 2006) or by attenuating neuronal activity of irrelevant feature representations (Chelazzi et al., 1993, Chelazzi et al., 1998, Lennert and Martinez-Trujillo, 2011). Corbetta et al. (1990, 1991) were amongst the first to report, that paying attention to non-spatial stimulus features results in enhanced neural activity in the cortical regions specialized in processing these features. Attention to non-spatial features elicits typical ERP-responses known as selection negativities (120-300 ms after stimulus presentation) or selection positivities with highest amplitudes over occipital scalp regions (Harter and Aine, 1984, Anllo-Vento and Hillyard, 1996, Anllo-Vento et al., 1998).

Based on single-cell-recordings in monkeys Motter (1994) found that attention to color increased activity of color-selective neurons in V4, if the color-stimulus in their RF was drawn in the neurons' preferred color. This firing-enhancement was independent of the localization of the focus of attention. Treue and Martinez-Trujillo (1999, 2004) report a similar finding in the motion-sensitive area MT. If the monkey attended to a certain motion-direction in one visual field, neurons tuned to that motion-direction showed an enhanced response even when their RF was in the opposite (unattended) visual field. Treue and Martinez-Trujillo (1999) developed the *feature-similarity gain hypothesis*, which states that FBA changes the sensitivity of visual neurons. Importantly, their studies revealed that the degree of enhancement is a function of the similarity between the attended motion direction and the cell´s directional preference. On the neuronal population level feature-based selection not only increases the selectivity for attended features by increasing the responses of neurons preferring this feature value, but also decreases that of neurons tuned to the opposite feature value (motion direction) (Martinez-Trujillo and Treue, 2004).

The operation of global FBA was also revealed at the neuronal population level. Boynton et al. (2006) observed that a single motion stimulus on one side of the visual field induced a motion aftereffect in the opposite visual field.

Saenz et al. (2002) demonstrated in a fMRI experiment spatially global neuronal modulation due to FBA (motion/color) across multiple early stages of cortical visual processing. Subjects solved a speeded detection task in one VF and neuronal activation increased for stimuli with the same feature value in the other unattended VF. The effect was visible across multiple early stages of cortical visual processing. The authors note that, “a feature-based mechanism of attention may thus work in parallel with a spatial mechanism to influence the earliest stages of cortical visual processing”. However, Maunsell and Treue (2006) hypothesized, that the similarity of the neuronal implementation of feature-based and spatial attention suggest a unified attentional system treating the location of a stimulus as one of its features.

In a visual search EEG/MEG-study Hopf et al. (2004) documented a short phase of parallel location-independent feature selection prior to target localization and selection. The task was a simple color-orientation conjunction search (Treisman and Gelade, 1980) with distracters. Half of the distracters shared an orientation feature (or feature value) with the target and half of them did not. A lateralized brain response indicating the presence of the relevant orientation feature preceded the N2pc (second negative deflection posterior contralateral) response by about 30 ms, and indicates the position of the target in space. The N2pc reflects attention shifts towards the target (Hopf et al., 2009) and has been shown to arise from source activity in extrastriate cortex (Hopf and Mangun, 2000, Hopf et al., 2002a, Hopf et al., 2004). The N2pc component can be seen as an index of attentional focusing (Kiss et al., 2008a, Kiss et al., 2008b, Leblanc et al., 2008, Ansorge et al., 2009). Hayden and Gallant (2005, 2009) support the idea that spatial and feature-based attention are mediated by discrete cortical substrates and suggest that both forms of attention act by enhancing the excitability of visual neurons. Priority of feature- or location-based selection may be flexible adjusted according to task demands.

As already mentioned above a very notable property of FBA is that it can enhance responses to non-spatial features outside the focus of attention, i.e. the selection of a feature at one location triggers selection of that feature at another location, which is referred to as *global feature-based attention*. This has been widely documented for monkeys (e.g. Martinez-Trujillo and Treue, 2004, Maunsell and Treue, 2006) and human observers (e.g. Saenz et al., 2002, Hopf et al., 2004, Boehler et al., 2011b).

Recent research revealed, that global FBA also occurs in the absence of feature competition in the focus of attention, but might be dependent on a simultaneous presentation of attended and distractor features having the same onset and offset (Bartsch et al., 2014). This study also revealed that global color-based selection is reflected by a sequence of two response modulations, i.e. an initial phase around 200 ms, which is thought to reflect the presence of a target-defining color (compare section 1.5 Task and Attention Control for the role of task sets), dubbed attentional template matching and a later phase around 280 ms, which was named discrimination matching, because it reflects the color selection at an unattended location/object as a result of the discrimination process in the focus of attention. Apparently, the later phase was localized more downstream in the visual hierarchy in ventral extrastriate cortex (V3/V4) than the initial phase, which was localized in lateral occipital complex (LOC - in monkeys presumably TEO), an area processing object information, giving rise to the assumption that global color selection works as a recurrent process in the backward direction from coarser to more fine-grained visual representations. This reminds of the proposal Hochstein and Ahissar (2002) made in their paper outlining vision in general. They suggest that for “vision with scrutiny” (attention) visual routines advance in reverse hierarchical direction in contrast to “vision at a glance” taking place at high-level areas.

1.3.3 Object-based Selection

To interact with things, we need to perceive our visual world in coherent unitary objects having many different features. If you want to grab a chair to sit down, you need to know which parts belong to the chair and which to the table or the environment.

As described in section 1.2 “Functional Anatomy of the Visual System”, vision in low-level visual areas, beginning with V1, fragments the visual scene into small featural details like texture patches and short contour elements. Ascending the ventral stream receptive fields of visual neurons become larger until they have the capability to represent larger parts of the visual scene. But how are different features like color, motion, and orientation, which are represented in diverse cortical areas, bound together to form a unified percept?

A widely accepted solution to the so called *“binding problem”* is proposed by the “integrated competition model” (Duncan et al., 1997, O'Craven et al., 1999). According to this model, directing attention to one feature of an object biases the processing of unattended features of that object. A further development of this model based on the observation, that objects meeting criteria of the Gestalt laws (Wertheimer, 1923), like similarity, proximity, connectedness or good continuation, may not be necessarily processed with the same speed (Jolicoeur et al., 1986). Roelfsema and Houtkamp (2011) proposed a two-part mechanism they dubbed *“incremental grouping”*. In a first process features represented by neurons with the same tuning shall be bound together. Afterwards the incremental part of the theory comes into play, because “base grouping” might not be sufficient to bind all necessary feature dimensions for an object, i.e. this will be a time-consuming and capacity-limited process requiring spreading neural activity over all neurons representing the corresponding image elements.

1.3.3.1 Electrophysiological Evidence

Experimental evidence for feature binding (O'Craven et al., 1999, Schoenfeld et al., 2003) showed that the neural representations of all other non-attended features, including the ones that were not relevant for the task are activated. In a visual search experiment Boehler et al. (2011b) measured ERPs and could demonstrate that the object-based bias for an irrelevant feature can also appear in another unattended object when it shares that feature with the target object, suggesting that the selection of irrelevant features is not confined to the attended object and acts in a more global way. The findings of Schoenfeld et al. (2014) proved further evidence for binding across feature dimensions to form a unitary perception of an object. In a MEG-study subjects were shown two superimposed moving dot arrays that were perceived as transparent surfaces. Subjects were asked to attend to only one of them on the basis either of color or speed of motion. The authors found a rapid sequential activation of the relevant and irrelevant feature modules depending on the specific task. MEG-waveforms showed increased responses in the motion-specific cortical area starting at ~150 ms after motion onset, when surface motion was attended, followed by enhanced activity in the color-specific area ~60 ms later on.

When surface color was attended the picture reversed and increased responses in color-specific areas could be measured prior to enhancements in motion-specific areas.

1.4 Contingent Attentional Capture

The differentiation between voluntary and involuntary attentional orienting is related to the distinction between exogenous vs. endogenous attention control (Posner, 1980), or between automatic vs. non-automatic attention control (Jonides, 1981). The notion of exogenous orienting is inspired from the neurological reflex. The concepts of automatic and exogenous control suggest that the control of selective attention lies outside of the organism, such that the stimulus itself attracts attention in a bottom-up fashion. The counterpart is called endogenous, non-automatic, voluntary or top-down control, where attention is shifted to locations, features or objects to meet the individual’s performance goals.

It should be noted, that shifting attention according to individual goals is regarded to be top-down, but must not necessarily be voluntary. The segregation between bottom-up and top-down is not strict, meaning automatic (bottom-up) attentional capture (cf. section 1.1, Yantis, 1996) can be influenced by top-down factors, which was demonstrated in a seminal paper by Folk and Remington (1992). They noted that previous studies of involuntary attentional capture always used distracter stimuli, that had the same stimulus properties which did also define the target. In their experiments Folk et al. studied attentional capture by carefully controlling the relation between properties of the distracter and the target. They tested two unique distracter properties (color, abrupt stimulus onset) against unique target-defining properties (again, color, abrupt onset). Confirming previous results, they found that when distracter and target properties matched, distracters captured attention. But when they did not match, even the abrupt-onset of a distracter did not capture attention. The critical point is the relationship of distracter properties to the target-finding properties. Folk et al. proposed that cognitive goals determine attentional control settings before the task, so that stimuli matching these settings will capture attention in the task. They dubbed their hypothesis contingent involuntary orienting hypothesis, because the reflexive allocation of attention is contingent on attentional control setting (cf. Pashler et al., 2001).

A whole body of follow-up studies confirmed the findings of Folk and Remington (Bacon and Egeth, 1994, Gibson and Kelsey, 1998, Lamy et al., 2004, Eimer and Kiss, 2008, Kiss et al., 2008a, Leblanc et al., 2008, Lien et al., 2008). Also notable to this regard is the influence of working memory on attentional capture. Recent evidence suggests that capture is stronger when working memory resources are reduced, e.g. due to a discrimination task. (Lavie, 2005, Fukuda and Vogel, 2009)

Recently the contingent capture hypothesis has been objected (Theeuwes, 2010). Theeuwes has put forward the hypothesis, that all salient stimuli in the visual field automatically attract attention bottom-up, regardless of the attentional set for a search task. Only after spatial attention has shifted towards the stimulus, disengagement of attention is subject to top-down control. But still, in this hypothesis the attentional set is important for the process of disengagement: If the attention-capturing stimulus resembles the target, disengagement shall be slow and effortful. Sawaki and Luck (2010, 2011, 2013) merged both hypotheses and called it “signal suppression hypothesis of controlled attention capture” (Sawaki and Luck, 2011). Like in the bottom-up saliency hypothesis by Theeuwes they propose that salient items are detected irrespective of top-down control settings, meaning that all salient items generate an „attend-to-me“ signal. Similar to the contingent involuntary orienting hypothesis they propose that top-down control settings can influence whether this attend-to-me signal actually leads to the allocation of attention.

Taken together, top-down descriptions may entail a selection bias for one or a set of simple target-defining features (e.g., color, orientation) and may also refer to a selection bias contingent on the general behavioral relevance of a target object, for example, its emotional significance, or association of reward.

1.4.1 Electrophysiological Evidence

Salient stimuli capturing attention evoke enlarged ERP-/ERMF-amplitudes of early visual components compared to stimuli that do not attract attention. Distractors also sharing features of the attentional set entail contingent involuntary orienting reflected by enhanced P1 and N1 amplitudes. For example, Arnott et al. (2001) provided evidence for orienting contingent on target properties in a search task with location unpredictable cues. Two conditions (abrupt onset and color) were compared.

In the onset condition (onset targets) color cues did not capture attention and in the color condition (color targets) onset cues did not capture attention. Response times as indicator for attentional capture were dependent on the location of the preceding cue (same or other position than target), but only in those blocks in which the cue shared the uniquely relevant target feature. An N1-component enhancement could only be seen for cue-stimuli matching the target features. Moreover, several studies have reported the appearance of an N2pc component as an index of contingent attentional capture. The N2pc (N2-posterior-contralateral) is known to reflect attentional focusing (Luck and Hillyard, 1990, Luck and Hillyard, 1994). Eimer and Kiss (2008) found an N2pc in a cue-target search experiment for cues sharing features with the target, not for cues that shared no feature. Other authors had similar findings (Leblanc et al., 2008, Lien et al., 2008).

Sawaki and Luck (2010, 2011, 2013) put forward the hypotheses that all irrelevant, but salient distractor items were detected in the visual system and therefore catch attention in a bottom-up fashion. If those stimuli were behaviorally irrelevant they could be overridden with top-down suppression only afterwards if needed. The existence of such an “attend-to-me” signal for salient distractor items was inferred from an observed ERP component called distractor positivity (Pd) instead of the N2pc component seen for attended stimuli. The Pd modulation Sawaki and Luck found in their experiments occurred irrespective of attentional focusing and was previously shown to reflect the suppression of distractors in a discrimination task (Hickey et al., 2009).

1.5 Task and Attention Control

Overt or covert visual selective attention can be measured as amplitude modulation in electrophysiological or magnetic brain responses in visual cortex areas (Figure 3). But how is attention guided to behaviorally relevant locations or features?

A widely believed idea is that these modulations seen in visual cortex are caused by an attentional control network, that integrates momentary behavioral goals in perception. Hopfinger et al. (2000) suggest such a system of top-down control of spatial attention that modulates activity in extrastriate cortex. The cues of a spatial cuing paradigm evoked fMRI responses in superior frontal cortex areas, the inferior parietal cortex, superior temporal cortex, as well as portions of the posterior cingulate cortex and insula. In contrast, targets and areas for visual processing of the cue showed different activations, so that the proposed network is likely to represent the source of attentional selection.

In natural scenes eye movements are essential for stimulus selection, so that saccade planning and directing attention to a location might engage similar or same mechanisms (Corbetta et al., 1998). PPC and lateral intraparietal cortex (LIP) are areas responsive for saccade planning and may also represent salience. Koch, Itty and Ullman propose the existence of a “saliency map”, which is able to guide attention faster to a salient stimulus in the visual scene than top-down influences could, because visual input would not have to be processed completely (Koch and Ullman, 1985, Itti and Koch, 2001). This hypothetical map is possibly located in posterior parietal cortex (PPC, see Figure 2) and should work as follows. Early stages of visual processing decompose the incoming visual input through feature-selective filtering processes and as a result feature maps emerge. These feed into a unique “saliency map” consisting of a two-dimensional (2-D) topographic arrangement of neurons that represent stimulus saliency throughout the visual scene. Feature saliency for different feature categories (color, motion, etc.) may merge into a superior saliency map. (Itti and Koch, 2001) Bisley and Goldberg (2003, 2010) see area LIP as a possible location for a similar “priority map” computing both, bottom-up and top-down inputs in order to represent overall behavioral relevance that can be used for attention and eye movements.

Moore and Armstrong (2003) expanded the idea that motor systems engaged in saccade programming provide the basis for covert visual attention and modulate processing not only in dorsal stream visual areas, but also in ventral stream areas like V4. Gilbert and Sigman (2007) go further in their review and describe top-down modulation as a general principle in all cortex areas, where selective attention with all its categories like features and objects is only one part next to expectation and the perceptual task. They suggest that any cortical area works as “adaptive processor” computing retinal bottom-up input and contextual and experience-dependent top-down feedback in a moment-to-moment process setting the cortex in a certain working mode – a “brain state”.

Top-down feedback to visual cortices is possible within the hierarchy to a lower area, and from known attention areas (in monkeys) as FEF, LIP, and PFC, which have connections to visual areas (reviewed in Baluch and Itti, 2011). Interestingly, area LIP might compute even higher cognitive information like behavioral value (Louie et al., 2011). In a recent review Gottlieb (2012) comes to the conclusion, that neurons in LIP, which are responsible for target selection encode the “relative value of alternative actions”. The area LIP gets input from PFC, an area dealing with a number of executive control processes like shifts of attention, or working memory and also likely the representation of reward (Goldman-Rakic, 1995, Miller and Cohen, 2001, Tanji and Hoshi, 2008, Wise, 2008). And the dorsolateral prefrontal cortex (DLPFC, Figure 2) in turn is associated with visuo-spatial working memory (Smith et al., 1996). According to Knudsen (2007) working memory is inevitably interconnected with top-down attentional modulations, because it does not only store information for some seconds, in doing this, it represents the objects of attention. And not to forget, in respect to visual search working memory is essential for holding the target in mind (Tanji and Hoshi, 2008).

Visual search and contingent attentional capture in general are based on attentional sets (Corbetta and Shulman, 2002) or *task sets* – mental programs that orchestrate performance of search and other complex tasks. According to Norman and Shallice (1986) behavior in familiar tasks is controlled by unconscious schemata, which select and coordinate the elementary processes that take place in task execution (cf. Meiran, 1996, Dosenbach et al., 2006).

Before every search task subjects get a detailed instruction and develop a specific task set making sure that in a moment-to-moment process the task is performed properly. Such a task set is part of executive brain functions or cognitive control processes that enable the brain to optimize the flexible use of limited cognitive resources to currently prioritized tasks. Our brain needs to detect environmental changes to allocate more cognitive and/or attentional resources to prioritize tasks when necessary.

Executive control may trigger overriding of habitual responses, shifts between different tasks or inhibition of distracting stimuli. Current research suggests that the anterior cingulate cortex (ACC) and the DLPFC play a special role in cognitive control. ACC is thought to monitor or detect a present conflict between task-relevant and task-irrelevant information and may exert executive control by selectively biasing processing in favor of task-relevant information. Alternative, ACC may just detect the conflict and then convey information to DLPFC, which then exerts cognitive control. (Mansouri et al., 2009)

Dosenbach et al. (2006) where able to extract top-down task set signals out of visual experiments and identified three different types of signals. One in the beginning of a task block to implement the task set, one to maintain it throughout the task and an error-related feedback-signal. They suggest that the dACC and the medial superior frontal cortex (msFC) play a core role in an executive control system. Furthermore, there has been broad evidence for the notion, that the role of dACC might not only lie in monitoring conflicts between task and distractors, but also in focusing attention on behaviorally relevant stimuli (Pardo et al., 1991, Posner and Dehaene, 1994, Weissman et al., 2005).

Importantly, in humans, top-down settings for task-relevant stimulus properties can be set by plain verbal instruction without resorting to the direct application of reward, which makes it easier to separate task- and reward-relevant top-down settings (Boehler et al., 2011a), but see section 1.8 “Effects of Reward on Visual Selection” for more details on the possible confound of reward- and attention-based experimental effects.

1.6 Learning and Reward

To review the whole topic of reward in all its facets including higher cognitive functions like decision making or overt behavior (Schultz, 2000) would go beyond the scope of this work. However, to think of attention as the only variable in visual sensory processing may fall short of the mark. True that an incoming visual stimulus has to pass attentional selection to reach consciousness or working memory. But reward may either shape attentional control or even exert direct neuromodulatory influence on stimulus selection as well (see section 1.8. “Effects of Reward on Visual Selection”). For instance the neuromodulator dopamine is besides its prominent role in subcortical reward mechanisms is also thought to facilitate learning (Schultz, 2000). By contrast, perceptual learning as a prerequisite for achieving practical skills is also in the visual domain classically thought to depend on practice, i.e. repeated presentation of a - normally attended - stimulus. But this view has been challenged by the finding that stimulus-reward pairing is sufficient to evoke perceptual learning effects of unconsciously perceived stimuli (Seitz et al., 2009). Taken together, in the triangular relationship of attention, reward and learning, depending on circumstances everyone dates everyone and sometimes all three go together.

1.6.1 Neural Correlates of Reward

In literature is often referred to a “reward system”. This term typically denotes several interconnected brain structures that process reward-related information. Traditionally, the reward system is thought to consist of two major pathways, the mesocortical and mesolimbic dopamine systems. Both pathways originate in the ventral tegmental area. The mesolimbic pathway connects to the nucleus accumbens in the ventral striatum, while the mesocortical pathway connects to the cortex, especially the frontal lobes. In their influential paper Berridge and Robinson (1998) review the role of these dopamine pathways. Their “incentive salience hypothesis” differs from other models in the assumption of a “hedonic” component, i.e. a difference between “liking” and “wanting”. In a first step a “hedonic activation” shall take place, followed by the association between stimulus and hedonic consequences as second step, and finally “incentive salience” shall be attributed to an event or stimulus.

They found that “dopamine-depleted rats still ‘like’ rewards, and still know the rewards they ‘like’. They simply fail to ‘want’ rewards they ‘like’.” (Berridge and Robinson, 1998) To stick to rats, the septal area became famous for an experiment from Olds and Milner (1954), where rats pushed a lever to stimulate themselves, and this made the idea of a reward circuit centered around nucleus accumbens and ventral tegmental area popular (Haber and Knutson, 2010). Unfortunately, more recent studies draw an anatomically and functionally more complicated picture. Haber and Knutson see a focus on midbrain areas and ventral striatum, which receives main cortical input from ACC and orbital frontal cortex and major dopaminergic input from the midbrain. Brain structures of this system include among others the cortico-basal ganglia system, Amygdala and Hippocampus.

Substantia nigra pars compacta and ventral tegmental area contain most of the dopamine releasing neurons, which distribute dopamine in a “normal” “tonic” or reward-related “phasic” mode (Schultz, 2000). Interestingly these phasic dopamine responses are not triggered by reward per se, but can rather reflect a ‘‘reward prediction error’’, reporting the difference between actually received and predicted reward (Schultz et al., 1997). But dopaminergic neurons encode far more than the prediction error, so that a recent proposal divides the neural population into salience coding dopaminergic and value coding dopaminergic neurons responsible for so different functions like general motivation, orienting, and cognitive processing or value learning, evaluation, and seeking, respectively, including also responses to none-reward events (Bromberg-Martin et al., 2010).

But note, that signals reflecting value might be ubiquitous in the brain (Vickery et al., 2011). In line with the nature of reward and value at large there is no single structure representing reward only. But for example, whatever the exact function of dopamine in reinforcement learning or motivation may be, it is of minor interest for this work that concentrates on the effects of reward on visual processing. The reward contingency of a stimulus is by then detected by the “reward system”. But if reward alters perception via attention or maybe a ubiquitous reward signal also biasing perception is worth to be considered in the following sections.

1.6.2 Perceptual Learning

Locals spot small frogs on rainforest leaves, where tourists just see a green hell. However, with training every subject improves skills of perception. Karni and Sagi (1993) found perceptual learning effects stable over years and attributed their findings to plasticity in early visual cortex. Evidence is mixed to the question to what extent increased performance due to perceptual learning stems from early-level modifications or is mainly attributed to improvements in higher-level readout stages. After all, both may be true and depending on task demands. Paradigms, where subjects have to make difficult discriminations of fine featural details may lead to plasticity in early visual cortex, while easy tasks over many locations and feature values suggest plasticity in higher representational areas. Paradigms like the one used in this work on the basis of easy to discriminate features, might also be learned independent of plasticity in visual cortex as stimulus-response mappings. (Roelfsema et al., 2010)

But it seems, that even though high frequency may signal ecological relevance, only practice is not sufficient for perceptual learning to occur. Stimuli have either to be attended (Ahissar and Hochstein, 1993, Jiang and Chun, 2001) or to be reward-associated, even when not attended (Seitz and Watanabe, 2005, Seitz et al., 2009). Perceptual learning can also occur for non-attended stimuli, that are even to weak to be perceived (Watanabe et al., 2001), but this might be also explained with reward. Subjects performed a task with rapid serial visual presentation of target digits on a background of a sub-threshold motion stimulus. Remarkably, subjects motion discrimination performance increased for the paired direction. Thus, a positive task outcome might generate an intern reward needed for pairing the attended stimulus with the subliminal stimulus (Seitz and Watanabe, 2005). But an external reward is also sufficient. In another experiment human subjects were deprived of food and water and then exposed to visual stimuli of which some were rendered unconscious by continuous flash suppression and paired with drops of water as reward. The direct association of the stimulus with a primary reward also seemed to evoke perceptual learning in the context of pavlovian conditioning in monkeys (Franko et al., 2010) and even in the absence of attention in humans (Seitz et al., 2009).

1.6.3 Perceptual Priming

“Priming describes the effect of a (sometimes subliminal) stimulus on subsequent perception of (other) stimuli and/or behavioral responses” (Fahle and Poggio, 2002). Perceptual priming also differs from perceptual learning in the durability of the effect, because priming effects usually vanish after tens of seconds (Fahle and Poggio, 2002). Even though perceptual priming is in most cases not attributed to any attentional mechanisms, it is an interesting phenomenon in respect to modulatory effects in extrastriate cortex ascribed to reward contingency in visual experiments.

In contrast to episodic or semantic explicit memory perceptual priming involves unconscious implicit memory (Schacter, 1987). Word-completion tasks are classical priming experiments. Subjects read a word list and after a delay period word fragments are presented, which they are asked to complete. Subjects show better performance for words that were previously shown to them even if they cannot remember the word list explicitly. The fact that small children and amnesic patients show veritable perceptual priming effects lead to the idea, that this form of memory does not rely on memory-circuits in medial temporal lobe, but instead on mechansims in perceptual cortex areas. (Tulving and Schacter, 1990)

The simplest form of priming is repetition priming. Every perceived stimulus is primed and if the same stimulus is experienced the next time, performance is enhanced. Studies investigating repetition priming with different methodologies could show that - while enhancing performance - perceptual priming decreases stimulus processing activity (Squire et al., 1992, Li et al., 1993, Gruber and Muller, 2002, Wig et al., 2005, Moldakarimov et al., 2010) possibly via sharpening of the stimulus representation in early visual cortex, which in turn leads to a more selective activation of up-steam neurons representing more complex stimulus properties in higher cognitive cortex areas (Moldakarimov et al., 2010).

Priming that improves performance is also called *positive priming* in contrast to the more complicated concept of *negative priming*, which weakens performance. Positive priming simply requires experiencing the stimulus, whereas negative priming means a slower or more error prone response caused by a previously ignored stimulus. Two major hypotheses try to explain negative priming. One popular model is a memory mechanism named “episodic retrieval model” (Neill et al., 1992).

This hypothesis states that ignored stimuli will be tagged “do-not-respond” and during memory retrieval the tag would cause a conflict. Another possibility is an attention-driven mechanism involving distractor inhibition (Houghton and Tipper, 1996).

Perceptual priming seems to be dependent on attention in a way that previously attended stimuli lead to the known performance increases and neural response decrease with repetition, while previously unattended stimuli can be associated with negative priming behavior and neural response enhancement linked to inhibition (Vuilleumier et al., 2005). In a visual scene with several similar items the target pops out in case it differs in one feature from the distractors. For example a red colored singleton pops out among green objects with the same shape. Priming also happens during visual search, which has been investigated for “pop-out” targets (Maljkovic and Nakayama, 1994). This kind of repetition priming was considered to be not influenced by top-down goals and settings (e.g. Theeuwes, 2006, Kristjansson, 2008), but reward contingencies do seem to seem to alter search and priming effects (Kristjansson et al., 2010), but see the following section for further elaboration on this aspect.

1.7 Effects of Reward on Visual Selection

Traditionally studies of visual selective attention investigate physical aspects of selection described with stimulus characteristics like luminance, contrast, color, motion, being an object or not, and so on. Non-visual contextual information like reward-association has only been studied more intense for one or two decades. Schultz (2000) mentioned “the possibility that the dopamine activation might encode a specific form of attention that is only associated with rewarded events”. Until now in the context of visual search research has failed to proof evidence for a direct modulatory impact of the reward-system on early sensory cortex areas bypassing top-down attentional control. But research is still in progress to define the role of reward and attention in visual stimulus processing.

1.7.1 Reward as (more or less) Independent Factor for Visual Selection

Hickey and colleagues (2010) managed to separate reward from target features in a visual search paradigm. Subjects searched for a shape singleton (target) among similar colored items and one color-singleton drawn in a different color (color-distractor). Color was completely task-irrelevant and subjects were given high or low reward upon correct target discrimination on every trial. Colors could swap from trial to trial, with the color of the target becoming that of the distractor or could remain the same. Meaning the distractor was either presented in the previously high or low rewarded color. The critical observation was that color distractors appearing in the color that was combined with high reward on a previous trial elicited an enhanced contralateral P1-response – an enhancement not seen when the same color was associated with low reward on the previous trial. A P1-enhancement typically reflects an effect of location selection associated with a gain-amplification of neural processing in retinotopically corresponding extrastriate visual areas (Hillyard and Anllo-Vento, 1998), suggesting that reward-relevance biased processing in extrastriate cortex, even though color was generally task-irrelevant and non-predictive as to the target´s location. The authors stress the point that reward does not only influence goal-directed behavior through strategy or attentional set, but has direct impact on visual stimulus processing.

This notion gets support from the finding, that reward may create salience in the oculomotor system causing the eyes to orient towards a reward-associated stimulus irrespective of individual goals (Hickey and van Zoest, 2012, Theeuwes and Belopolsky, 2012).

Other authors also argue that value-based factors like the reward-relevance of a stimulus may be separable from task relevance at the level of sensory selection (Shuler and Bear, 2006, Seitz et al., 2009, Weil et al., 2010, Arsenault et al., 2013).

Shuler and Bear (2006) trained rats to expect reward (water after x licks from a water tube) after full VF illumination by face mounted goggles. Half of all trials were unrewarded. The time span to reward delivery was longer for right eye stimulation than for left eye stimulation. Using single cell-recordings they found that naive rats just showed a response to visual stimuli, whereas the activity of V1-neurons from experienced rats correlated with reward time associated with the light cue. The observed post-stimulus activity appeared to be related to reward-time prediction and not to reward delivery per se, because it also occurred during the unrewarded trials. In a follow-up study Chubykin, Roach, Shuler and Bear (2013) identified plastic changes in primary visual cortex underlying reward-timing activity. In their experiments with rats they selectively removed cholinergic input from basal forebrain to V1 with the result that cue-reward intervals could not be learned any more, but previously learned intervals still showed intact expression. These results show, that cholinergic input to V1 does not represent a direct visual stimulus-reward-association, but the finding of ACh-dependent conditioned learning of reward-timing as early as in V1 is striking. Consistent with the finding that visual neurons predict reward, Weil et al. (2010) also found distinct effects for reward and spatial attention with fMRI in human visual cortex. In both hemifields gratings were presented to subjects, which had to discriminate the orientation in one visual field and to ignore the other similar grating. Auditory feedback was given on the amount of reward for every correct trial to avoid stimulation of visual cortex. Feedback on reward increased the blood-oxygen-level-dependent (BOLD) signal in area V3 in spite of the missing visual stimulation. In V1 enhanced activity due to reward was found depending on the previous trial, which had to be rewarded.

Shuler and Bear (2006) found V1 activity rather depending on reward-timing than reward itself, while Weil and colleagues (2010) failed to find cue-specific reward-modulation in “early” visual cortex. Having in mind that there may be differences across species (rat, monkey, human) to this regard, Arsenault et al. (2013) provided more direct evidence for reward cues and reward itself modulating visual cortex areas in monkeys, including at least V2, V3, V4 and TEO, independent of attention. Monkeys were trained to perform a fMRI experiment with a 2 x 2 factorial design. With the same probability juice reward could be delivered after a cue or without cue, and trials without reward could be cued or not cued (fixation). When delivering reward without visual stimulation, they had the counterintuitive finding of a decreased BOLD signal in visual cortex. Visual attention in the absence of visual stimulation is thought to induce an enhanced BOLD response (Kastner et al., 1999). That reward, instead, lead to a relative attenuation, is suggested to not represent stimulus deactivation, but rather an increase in stimulus information, which could be mediated through a decrease of baseline activity and a subsequent boost of the signal-to-noise ratio. Additionally, the authors speculate on the basis of the observation of the cue-reward association being strengthened by un-cued reward events, that there is a mechanism turning an unspecific dopamine signal in visual cortex into a stimulus-selective one. Similar to the theory of perceptual learning by Roelfsema, Oyen and Watanabe (2010) claiming that reward as a reinforcer causes diffuse distribution of the neuromodulators ACh and dopamine gating plasticity in order to enable attentional feedback to “highlight the chain of neurons” from perception to action. Arsenault et al. (2013) propose an interplay between sensory representation of the cue and reward feedback to “tag” the stimulus representation. In a second step, a diffuse reward signal generated by uncued delivery of reward may interact with the previously “tagged” stimulus representation explaining the selective visual cortex modulation they observed at the location of the cue. That reward might be able to bias visual selection independent of attention gets support from the elegant behavioral study from Seitz et al. (2009) already mentioned in section 1.6 “Learning and Reward”. Human subjects deprived of food and water viewed stimuli rendered unconscious by continuous flash suppression but paired with drops of water as reward. Stimulus-reward pairing seemed to evoke perceptual learning in the absence of attention.

1.7.2 Reward as Determinant of Attention

The connection of reward and attention has been made for area LIP and PFC for instance, because they are known for their role in guidance of attention as well as for coding of reward. A possible candidate for the encoding of reward to modulate visual attention lies in PFC. The LPFC plays a role in a number of executive control processes including shifts of attention, working memory, strategy implementation, representation of rules/categories/objects, and response inhibition among other functions (for detailed reviews, see Goldman-Rakic, 1996, Miller and Cohen, 2001, Tanji and Hoshi, 2008, Wise, 2008). PFC has close connections to LIP and neurons in LIP also show modulations due to reward (Platt and Glimcher, 1999). Peck et al. (2009) trained monkeys to make a saccade to a target stimulus and additionally presented a task-irrelevant cue signaling reward and a second cue signaling no reward for the trial. Even though the cue was uninformative for saccade planning, neurons in LIP encoded an attentional bias toward the location of the reward-cue and inhibition of the location of the non-reward cue. These findings suggest area LIP to code the "value of information" and convert this information into top-down attention. (reviewed in Baluch and Itti, 2011)

Lets assume that reward alters deployment of selective attention, how then is reward bound to a visual feature, if cognitive cortical areas encoding value or reward-relevance per se are blind for fine-grained visual features? Baluch and Itti (2011) state, that cortical areas like LIP, FEF or a subcortical structure like the SC might normally be "feature agnostic", while visual cortical areas, IT and PFC might operate in a "feature-committed mode". They suggest, that the pulvinar works as a bidirectional translator and converts featural top-down signals into coarser feature-agnostic signals and vice versa.

Recent literature proofs an association of reward with visual features and objects, so that major effects on visual selection and task performance can be observed (for review see Chelazzi et al., 2013). In studies using the spatial cuing paradigm (Posner, 1980) (see section 1.3.1) performance changes due to reward indicate facilitation of relevant and de-emphasizing of irrelevant input (Engelmann and Pessoa, 2007, Engelmann et al., 2009).

Studies with a training phase - test phase - design showed a similar performance effect of a learned reward contingency for cues (Anderson et al., 2011a, b), and even for non-salient cues (Failing and Theeuwes, 2014). On a trial-to-trial basis reward also affected performance. A (high) reward-associated feature (color) becoming a target feature in the next trial resulted in faster response latencies in latter trial (Hickey et al., 2010). The attentional phenomenon of negative priming (for Perceptual Priming see section 1.6) - in this case slower performance for a subsequent target stimulus after presentation of a prime stimulus containing both distracting and target features – could be observed for high reward stimuli in contrast to low reward stimuli (Della Libera and Chelazzi, 2006). In a follow-up study the learned reward association induced negative priming also several days later even though the test phase did not involve any delivery of reward (Della Libera and Chelazzi, 2009). “Pop-out priming” (section 1.6) results in better performance on successive trials, when singleton properties are repeated and is thought not to be influenced by top-down voluntary control or task sets (reviewed in Kristjansson et al., 2010). However it seems to be prone to changes of the reward level, as performance improved with high reward compared to low reward even without explicit knowledge of reward associations (Kristjansson et al., 2010). These findings of implicit biasing suggest that reward has a direct modulatory impact on visual attentional selection (Hopf et al., 2015).

Behavioral goals and value influence attentional control, but the question remains *how* reward information exerts its influence on visual stimulus processing. Maunsell (2004) explicitly alluded to the risk of confounding reward and attention effects under experimental conditions. Especially in animal research the reward- and attention experiments are constructed similar and animals are rewarded for performing attention tasks. He emphasized the importance to distinguish between “neuronal signals related to expectations about future rewards” and “those related to attention to particular locations, stimuli or stimulus features”. Since this “admonition” ten years ago, research has changed direction to this regard. In a recent article Chelazzi and coworkers reviewed many experiments and proposed that “rewards ‘‘teach’’ visual selective attention so that processing resources will be allocated to objects, features and locations which are likely to optimize the organism’s interaction with the surrounding environment and maximize positive outcome” (Chelazzi et al., 2013).

Depending on the specific task this shall come about either by enhanced motivation influencing strategic attention control, or by a direct increase of stimulus priority during attentional selection. The latter is thought to be a mechanism based on learning, because effects are measurable even when reward is not part of the task anymore (cf. Della Libera and Chelazzi, 2009).

A growing number of studies – some of them were mentioned above - document the impact of reward on behavioral performance and visual sensory processing leaving open the question if these effects arise from same or different modulatory influences in visual cortex as the ones for visual attentional selection. (Buschschulte et al., 2014, Hopf et al., 2015)

Some authors found that stimuli with reward-relevance are processed like attended stimuli (Della Libera and Chelazzi, 2009, Kiss et al., 2009, Franko et al., 2010, Stanisor et al., 2013). In a single-cell study with two macaque monkeys Franko et al. (2010) investigated if a rewarded stimulus would be processed different than a non-rewarded stimulus. They found an increased neural response in local field potentials (LFP) to simple stimulus–reward pairings in area V4 outside the context of a task and relate an early modulation to enhanced attention and a later modulation to perceptual learning. Stanisor et al. (2013) also recorded from neurons in macaque monkeys performing a curve-tracing task with different levels of reward. In earliest sensory processing levels they found that firing effects due to selective attention and reward were indistinguishable in terms of changes in neural firing rate and latency. They suggest, that reward and attention depend on the same modulations in V1, because reward and attention effects could be observed in the same neuron.

Contrary to animal experiments in humans top-down settings for task-relevant stimulus properties can be set by plain verbal instruction without resorting to the direct application of reward, which makes it easier to separate task- and reward-relevant top-down settings. Kiss et al. (2009) could show enhanced N2pc-effects in ERPs of human observers for search targets paired with greater rewards compared to targets paired with less rewards. In their experiments all targets were rewarded. The results of this and other studies (e.g. Della Libera and Chelazzi, 2009) combining value information with target information are compatible with the interpretation that reward alters attentional selection.

2 Hypotheses

The literature on the role of reward in vision is expanding, but how reward influences early visual stimulus processing is still under debate. Attention to task-relevant features leads to a biasing of sensory selection in extrastriate cortex. The question is, if this is also true for reward-associated stimuli and if so, if these sensory effects are mediated by attentional mechanisms or arise from separable modulatory sources. To address this issue properly, top-down settings defining reward-relevance were separated from those defining task-relevance. The state of neural biasing for the target- and reward-relevant color feature was assessed with analyzing the neuromagnetic brain response under task-relevant conditions and under task-irrelevant conditions. In Experiment 1 and 2 in between search-frames asynchronously presented irrelevant color probes drawn in the target-defining color, the reward-relevant color, and a completely irrelevant color as a reference were part of the contingent attentional capture part of both experiments, while unattended distractor stimuli presented within the search task were analyzed under task-relevant conditions. The variation of reward magnitude addressed the question, whether the prospect to gain higher reward would alter the processing of reward-relevant color-probes. The null hypothesis for the probe analysis was, that the reward-color would lead to an enhanced response comparable with the one for the target-color (which was not the case).

The fixed target position in the third Experiment enabled a direct comparison between the effects of the target-, and the reward-color under task-relevant conditions. Here the null hypothesis was a bias for the reward-color (which was observed). Reward effects were analyzed in respect to the phenomenon of global feature-based selection under the hypothesis that reward effects will overlap with those of feature-based attention.

Overall, this work contributes to the assumption that reward is not just perceived and then alters motivational states of higher cognitive brain areas, but under certain conditions also alters sensory perception itself.

3 Methods

3.1 Magnetoencephalography Basics

How to investigate the neural activity in visual brain areas non-invasively with sufficient temporal resolution? One way is to measure electrical potentials over the human scalp another way to measure magnetic fields. Both are oriented perpendicular to each other (right-hand rule). Hans Berger invented the Electroencephalography technique, the EEG and published his discovery in 1929 (Berger). Almost 40 years later in 1968 the first magnetoencephalographic signals were measured by David Cohen (1968). To study event-related mental events with EEG only became possible when a small computer called CAT (“computer of average transients”) came into use toward the end of the 1950s (Eiselt, 1995). It was summing up potentials evoked by repetition of equal stimuli, which is still an up-to-date method to uncover the invariant electric answers to the stimulus that is hidden in the background EEG. After Zimmerman et al (1970) had developed the SQUID (superconducting quantum interference device) Magnetoencephalography (MEG) could be used analogue to EEG. SQUIDs detect tiny magnetic fields and translate them into electrical current, which then can be measured. At 10 femtotesla ($1fT = 10^{-15}$ tesla) for most cortical activity and about 100 fT for the human alpha rhythm, the brain's magnetic field is considerably smaller than the ambient magnetic noise in an urban environment, which is on the order of 108 fT. This is the reason for the magnetically shielded chamber used for all MEG-experiments. In favor of MEG it has to be mentioned that magnetic fields are less distorted than electric fields by skull and scalp (resistors), which results in a better spatial resolution of the MEG.

A central problem in assessing the neuro-electric/-magnetic brain response in human observers is that magnetic/electric fields of a single experimental trial do not stand out from spontaneous background activity. Measuring and averaging event-related potentials (ERPs) over the human scalp solves this problem and maps brain activity with high temporal resolution (milliseconds-range).

ERPs are obtained from the electroencephalogram of the whole cortex and averaged afterwards according to stimulus conditions (e.g. average all ERPs evoked by blue stimuli, by red stimuli and so on). The analogue method is to measure event-related magnetic fields (ERMF) with MEG. Both ERPs and ERMFs originate from ionic electrical currents across the membranes of active neurons, more precisely the summation of these currents. The electrical current across the membranes of a pyramidal cell in cortex elicit an electrical dipole. Pyramidal cells are oriented orthogonal to the cortex surface and parallel to each other. The excitatory or inhibitory postsynaptic potentials (EPSP, IPSP) of pyramidal cell assemblies produce measurable summation potentials. This is referred to as “open field situation” so that a detectable signal stands out from surrounding brain activity. Activity generated in brain structures like the thalamus cannot be detected with MEG, because they have irregular oriented neurons (“closed field situation”) and their small electric currents do not add up to a macroscopic current.

While MEG and EEG provide very high temporal resolution another important issue is to localize the sources of brain activity. This requires mathematical models for estimating the localization of current sources based on the measured electric/magnetic field distribution. But here is a computational problem, because the measured field distribution can be explained by many different source configurations in the brain. This so-called electromagnetic inverse problem (Helmholtz, 1853) can only be solved by introducing a priori assumptions about the generation of MEG (or analogous EEG) signals in the cortex (Michel et al., 2004). The key to rendering the inverse problem solvable in a reasonable way was to introduce anatomically realistic assumptions. To this end CURRY 6.0 (Compumedics Neuroscan, Charlotte, NC, USA) was used to minimize errors due to the inverse problem.

Brain activity was visualized in two different ways in this work. Figure 5 shows an example for a topographic map (a) containing the distribution of MEG field potentials, while CURRY-calculated spatial maps (b) show the result of mathematical source computation.

(a) Topomaps (topographic maps) plot MEG data (in fT) on a standard head shape by interpolating between amplitude measures at 248 MEG-sensors at a given time-point. Areas in red colors have positive values and indicate magnetic efflux, while areas in blue have negative values and indicate magnetic influx. In a typical constellation efflux and influx may represent the same underlying source. The exact source location, however, cannot be inferred by merely inspecting a magnetic field distribution.

(b) CURRY uses spatial filters, like the MNLS method (minimum norm least squares), to estimate brain activity at an arbitrary defined position in the cortex. This computation in every defined volume element of the cortex generates a 3-D-surface distribution of neuronal sources underlying the measured magnetic field distribution. The location of highest current source density (in µA/mm^2) corresponds with the location with the highest probability of brain activation (at a given time).

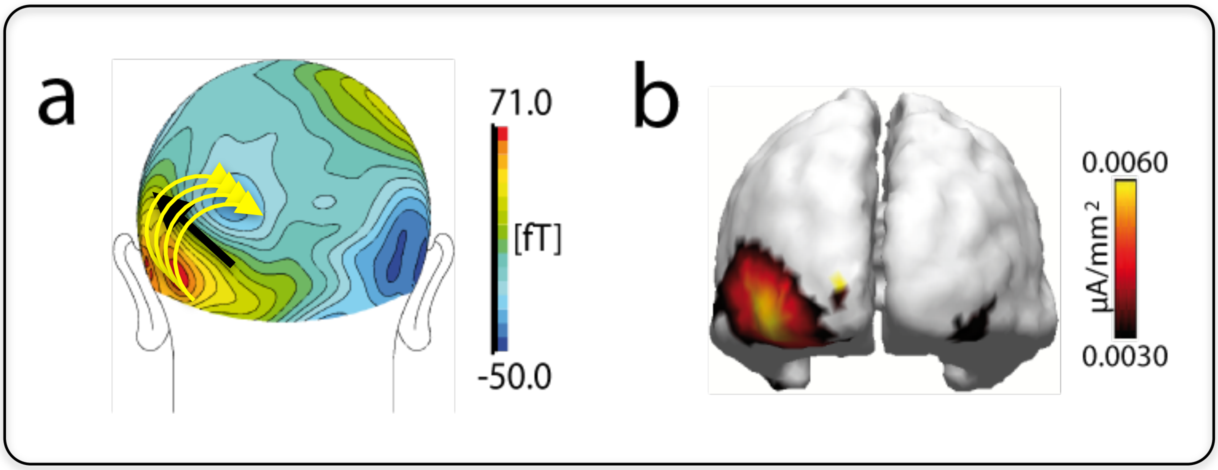

Figure 5: Visualized field distribution and corresponding source localization. The MEG-response elicited by a flash-stimulus presented in the right VF. The topomap (a) shows the magnetic field distribution for contralateral occipital brain activity. Because vision is represented occipital a view from the back is appropriate. The black arrow indicates the approximate current source (dipole), while the yellow arrows depict the magnetic field. Magnetic influx and efflux are represented in a blue-to-red scale in fT, deeper colors standing for higher field strength. Based on the same MEG-data the electrical source localization is shown in a 3D-surface distribution (b). The current source density distribution (µA/mm^2) was estimated with CURRY 6.0. In a black-to-yellow scale, yellow stands for maximum source density. Highest activity is also seen contralateral to stimulus presentation, but compared to the topomap precisely located lateral occipital in extrastriate cortex.

3.2 General Methods

In this section details of the methodological background regarding all experiments will be summarized. Specific information regarding the particular experiments and subjects will be given in the following experiments section. Experiment 1 and 2 (see also methods in Buschschulte et al., 2014) both follow the same basic principles, whereas in Experiment 3 (see also methods in Hopf et al., 2015) a variation of the color search task of the first two Experiments was used and will be explained separately.

3.2.1 Stimuli and Task – Experiment 1 and 2

The basic paradigm for both experiments consisted of two components: (1) A search for a color-defined target (search task) to establish a task set, i.e. associations with task-defining and reward-defining features, and (2) a probe-stimulation phase to assess the sensory biasing for the selection of the task- and the reward-related color during a task-irrelevant phase of the experiment.

(1) Stimuli of the color search task were double-colored 3D spheres as shown in Figure 6, that subtended a visual angle of 2.7°. Each stimulus frame contained a fixation cross (0.1° diameter visual angle) and two spheres, one presented in the left VF and one in the right VF centered at a distance of 5° to the left and right from fixation and 2.7° below the horizontal meridian. Each sphere - divided vertically into two halves – was composed of two colors taken from a set of five colors (red, green, blue, yellow, grey), which were randomly assigned to the left and right half of the spheres. All half-spheres in a search-array were always drawn in different colors. Both spheres appeared on a homogenously grey colored background (luminance: 24 cd/m2). Colors had following luminance values (in cd/m2): red = 24, yellow = 85, green = 80, blue = 9, grey = 48. Spheres were designed with Matlab (MathWorks Inc., Natick, MA, USA).

Subjects read an instruction before the task and practiced it before recording a session. Central fixation had to be maintained throughout the task. Figure 6 explains the task requiring subjects to report the location of the previously defined target-color.

The half-sphere drawn in the target-color could occur either on the left or the right side of the sphere. Subjects had to report the side of the target-color within the sphere by two-alternative button press of the right hand (index finger: left; middle finger: right) as fast and accurate as possible. On each trial, the target-color (red in Figure 6) was assigned to one of the four half-spheres, while three of the other four colors were assigned to the remaining half-spheres as follows. A second color was defined being the reward indicating color (green in Figure 6).

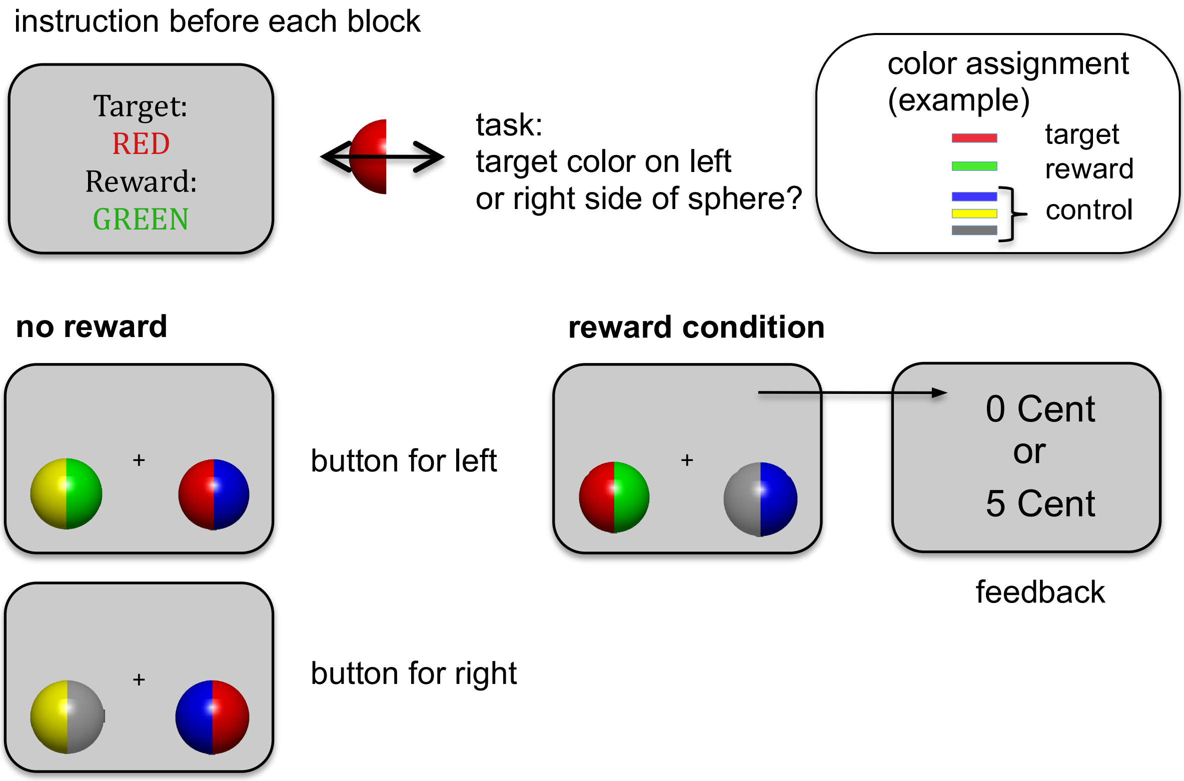

Figure 6: Experimental design (search task). Subjects were instructed before each trial block, which color would be the target-color (here red) and which would indicate reward (here green) when combined with the target. The task was to detect the target-color in the sphere in the left or right VF and than to decide if it appeared on the left or right side of the sphere. An example for correct responses is illustrated in the two search arrays on the left. The two arrays also show examples for non-rewarded trials. A rewarded trial is shown on the right. The left sphere is composed of target and the reward-color. The immediate feedback for a correct button press would be "5 Cent". For a slow or incorrect response "0 Cent" would be displayed.

Reward was delivered upon correct performance in case the target-color was combined with the reward-color in the target-sphere (red and green at right-hand side of Figure 6 “reward condition”, 1/3rd of all trials), while a combination of two irrelevant colors (grey and blue) appeared in the distractor sphere.

Two thirds of all trials were not rewarded (Figure 6, left “no reward condition”). Here, the target-color was randomly combined with one of the three control-colors (blue in the example in the array left, down). The distractor sphere could either contain a combination of the remaining control-colors (grey and yellow, bottom left in Figure 6), or one half-sphere of the distractor could be drawn in the reward-color (i.e. green in the example). The two different distractor conditions were equiprobable for non-rewarded trials. In case the reward-relevant color appeared in the distractor (upper search frame in Figure 6 “no reward condition”), no reward was given. Notably, the number of rewarded trials was set to a comparably low proportion of one third of the trials to minimize the incentive for subjects to take the specific combination of target- and reward-color as defining the target. Such combined target definition is more likely to occur with a higher proportion of rewarded trials and would clearly undermine the present aim to dissociate task- and reward-relevance.

In case of a rewarded trial a correct button press was rewarded with 5 Eurocent or 10 Eurocent in Experiment 2, respectively. After every reward-trial subjects received immediate feedback “5 Cent” (or “10 Cent”) for a correct response, or “0 Cent” for a false or omitted response. The amount of gained money was added up and paid after completion of the session.

(2) The contingent involuntary orienting part of the experiment was implemented as shown in Figure 7 a). In 50 % of all trials a to-be-ignored, but nevertheless attention-capturing square (the probe) was flashed for a duration of 50 ms between the search-frames in the same position as the spheres. This probe subtended 1.8° x 1.8° visual angle and could randomly appear either in the left or the right VF position. Colors were randomly assigned to the probe according to respective conditions. One third of the probes were drawn in the target-color, one-third in the reward-color, and one-third in the remaining “control”-colors. A probe was never directly followed by another probe.

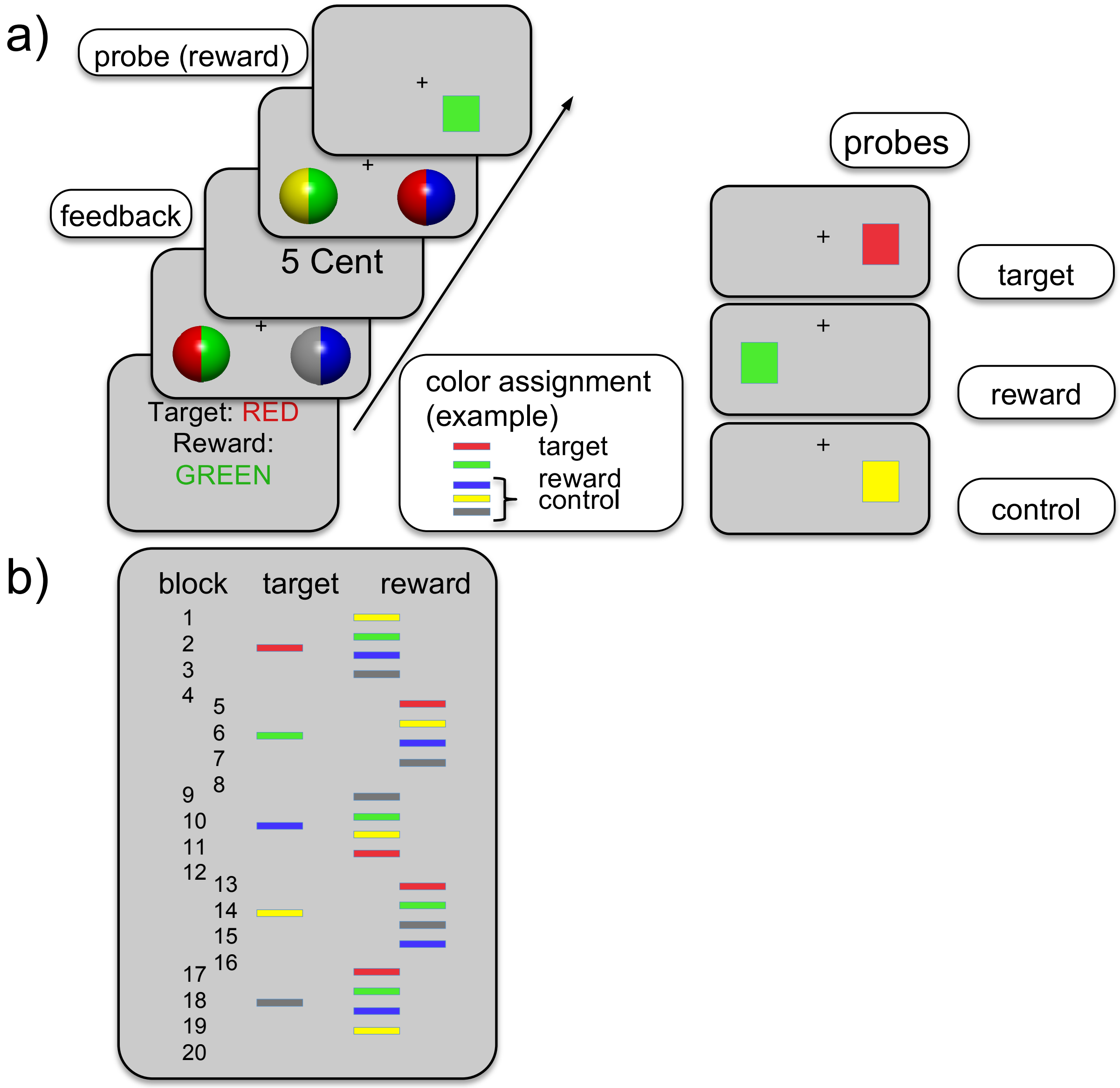

Figure 7: a) Experimental design and color assignment (probe-presentation). The presentation of search frames was randomly interleaved by the unilateral presentations of a color probe, which could only be presented after a search frame (including feedback). Also in a random order, probes were presented either in left or right VF. For example, picture a) shows the color-assignment for block 2: Target-color is red, reward-color green; blue, yellow and grey remain control-colors. On the right (b) the color combinations for all 20 blocks is shown. Subjects searched for a red half-sphere as target in block 1-4, reward-relevant color was yellow in block 1, green in block 2, blue in block 3 and grey in block 4. After 4 blocks the "target-color" changed into green for another 4 blocks and the "reward-color" from red in block 5 over yellow and blue to grey in block 8 and so on till all colors served as target- and reward-relevant color in every possible combination. For clarity respective control-colors are not depicted. For instance in block 20 the "control-colors" would be red, green and blue, because grey and yellow are assigned to target and reward.

Figure 7 a) down left shows an example for an instruction presented on the screen in order to inform subjects about the actual target and reward for the experimental block to come. Subjects decided individually, when to start the next block. As mentioned before the experiment consisted of the search task and the probe-presentation. The electromagnetic response for both parts was analyzed separately in the following way.

The MEG-response to the color-probes was analyzed as a function of their color being associated with “target” or “reward” relative to no association (“control”). Probes were always task-irrelevant. The comparison “target” versus “control”, and “reward” versus “control” was taken to reveal neural processing depending on the target and/or reward association of the colors, respectively.

With regard to their assignment to the experimental conditions, all five colors were counterbalanced. Figure 7 b) shows the block design of the color-search task for all experiments. One session consisted of 20 blocks. The target-color remained constant for 4 blocks, while reward-color changed in every block. For example in block 9, target-color was blue, reward-color was grey, and the remaining three colors (red, green, yellow; not shown in Figure 7b)) served as control. In sum, each color served as “target” and “reward” for the same duration of time.

The MEG-responses to search frames (spheres) were analyzed according to reward-color-presentation as shown in Figure 8. Only non-rewarded trials (lower two search frames) were analyzed as a function of whether the reward-color was present or absent in the distractor-sphere. The dashed circles mark the target-sphere and attended VF. To assess neural biasing for the target-color a different experimental design becomes necessary, which was realized in Experiment 3.

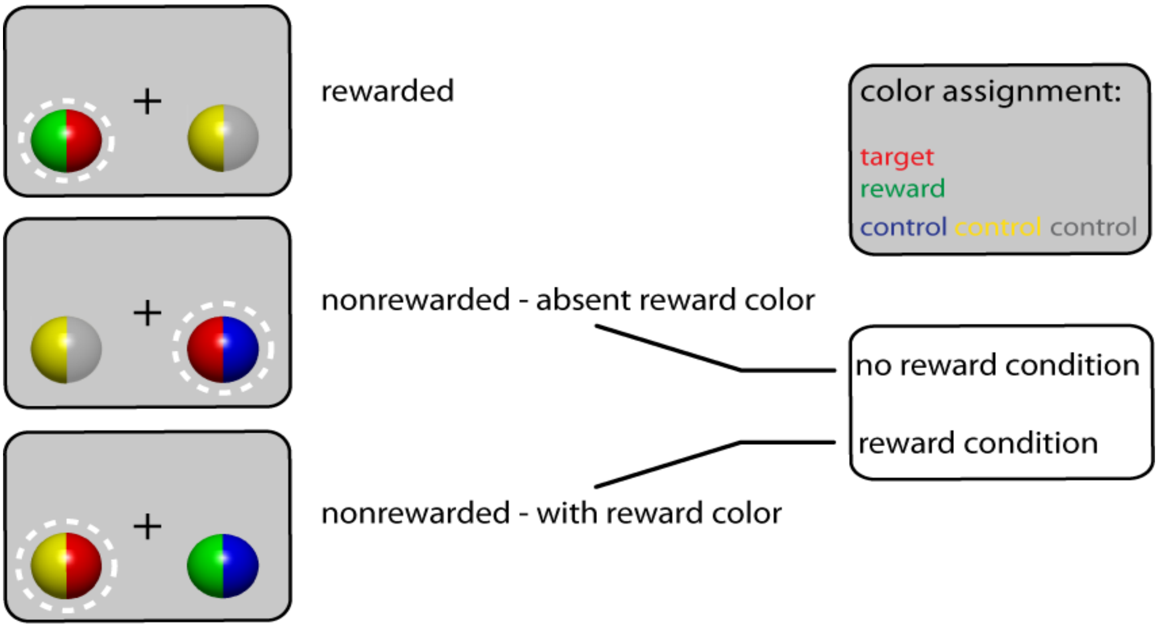

Figure 8: Conditions for the analysis of the MEG-responses to search frames of Experiment 1 and 2. Exemplary search frames are shown for the same color assignment used in previous figures. Containing the target-color the encircled spheres are marked task-relevant. Two conditions of the non-rewarded trials in the two bottom search frames were analyzed in respect to presence or absence of the reward-color in the unattended distractor sphere (no dashed circles).

Timeline and duration of stimulus-presentation are illustrated in Figure 9.

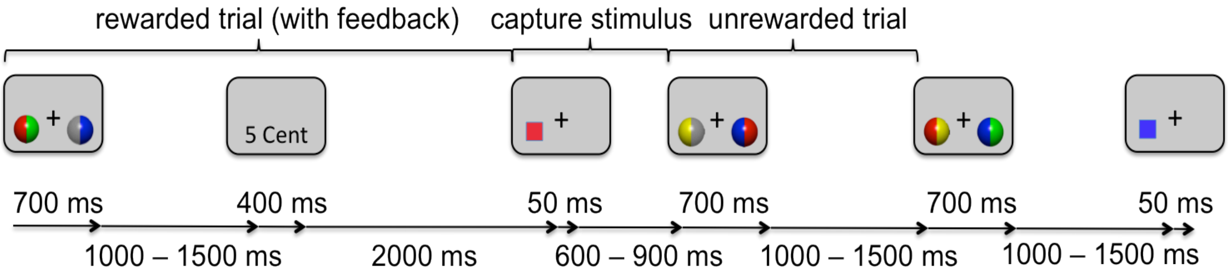

Figure 9: Timing of stimulus presentation. Search arrays were presented for 700 ms followed by an inter-stimulus-interval (ISI) randomly varied between 1000 and 1500 ms. In the example shown here the subject made a correct response to the rewarded search frame far left and the feedback "5 Cent" came up after 1000 – 1500 ms. In the following interval of 2 seconds (also blinking pause) the fixation cross reappeared after 1 second to secure fixation for the following stimulus presentation. The following frame could either be a search array or a probe stimulus. In case of the non-rewarded search frames 2 and 3 no feedback was shown. In between a probe (red probe in the middle of the figure) and the next search frame the ISI varied between 600 and 900 ms.

In Experiment 1 and 2 every block lasted for 2,5 minutes. Due to an inter-stimulus-Interval (ISI) varying from 1000 to 1500 ms or 600 to 900 ms after probe-presentation stimuli were presented irregularly in time preventing subjects from establishing a response-rhythm. The 2 seconds of feedback-pause after rewarded trials could be used for blinking. Probes were flashed for 50 ms, search frames were presented for 700 ms, and feedback-frames for 400 ms. Randomized presentation of search frames and interleaving probe frames made all stimuli unpredictable to subjects.

3.2.2 Stimuli and Task – Experiment 3

The third experiment (cf. methods in Hopf et al., 2015) aimed at a direct comparison between the neural modulations underlying the reward-associated and the target-associated color outside the focus of attention during target-discrimination. Apparently such situation is impossible to accomplish with a typical visual search task. The setup of the previous experiments was modified to allow a fixed target location in the left VF, but leaving the overall stimulus configuration comparable.

Without visual search subjects did not need to localize the target sphere based on target-color, only to discriminate the position of the target-half-sphere within the left sphere. Therefore it was possible to present both, the target and the reward-color, in the unattended right VF, and to compare the brain response elicited by respective colors. Otherwise the sphere stimuli were identical to the ones used in the first two experiments. Timing of stimulus presentation was also the same with the exception that no probe stimuli were presented. As in experiments 1 and 2 subjects had to report whether the target-color appeared on the left or right side of the target sphere with a two-alternative button press of the right hand (index finger: left, middle finger: right). Subjects read an instruction before the task and practiced it before recording the session. And also subjects were informed about the colors defining target and reward at the beginning of each experimental block. Colors were counterbalanced across conditions (see Figure 10).

In 25 % of all trials target- and reward-color were presented together in the left-hand sphere, i.e. they were rewarded trials and excluded from MEG-data analysis. Figure 10 depicts the four non-rewarded conditions comprising four distractor-configurations in right VF that were examined.

The color assignment in this example is like in the examples before: Target is red, reward is green, blue, yellow, and grey are control-colors. The dotted circle indicates the attended target-location in left VF. The uppermost array shows the control condition (C), i.e. the unattended sphere in the right-VF contains two control-colors, here yellow and grey. In the array below, the target-color (red in the example) is not only presented in the task-relevant left VF, but also in the distractor sphere together with a control-color in right VF characterizing the target condition (T). The third frame from above shows the situation with the reward-color (here green) appearing in the distractor sphere (R). At the bottom both, the target- and reward-color are presented together in the distractor sphere (T&R).

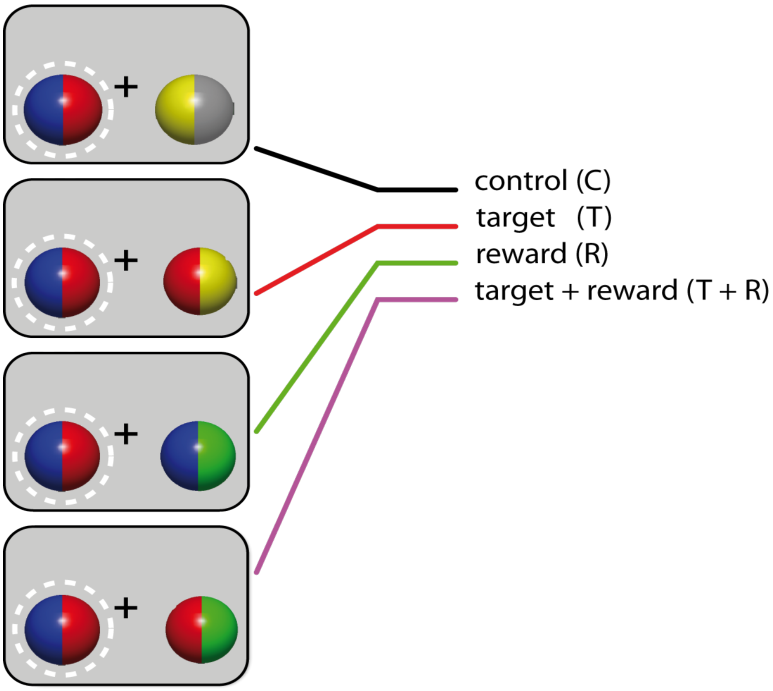

Figure 10: Distractor conditions of Experiment 3. While fixating the center cross subjects attended the sphere in left VF marked with a white dotted circle to localize the position of the target-color. Subjects were asked to report with a button press whether the red half was on the left or right side (here always on the right side). In this example red served as target-color and green as reward-color. On the unattended right VF color examples for four different distractor conditions are shown. (C) Control condition: the distractor sphere could either contain two irrelevant colors in the control condition, (T) Target condition: the distractor contained the target-color + a control-color (R) Reward condition: the distractor contained the reward-color + a control-color (T + R) Target and reward condition: the distractor contained both the reward- and target-color.

Each subject performed 20 blocks and the assignment of target-, reward- and control-color was changed from block to block as explained for Experiment 1 and 2 (see Figure 7 b). Block design and timing (except that no probe was presented) were identical to Experiment 1 and 2. One block lasted for 3 minutes. The amount of reward to be gained for every correct answer to a rewarded trial was 5 Euro-Cent with an immediate feedback presented to the subjects.

3.2.3 Data Acquisition and Instruments

Figure 11 shows the recording of MEG-signals in a magnetically shielded room by using a BTI Magnes 3600 WH 248-channel whole-head device (4D Neuroimaging, San Diego, CA; USA).

Figure 11: Experimental setup. The cryostat with the MEG-sensors resides in the magnetically shielded room. The picture shows me as a subject sitting on a bed under the cryostat, wearing an EEG-cap with the response box lying on her lap. The search array with two spheres visible on the backside of the screen is presented at 1 m distance to the subject´s eyes.

Besides the 248 SQUID sensors that register brain activity, reference sensors (5 gradiometer and 6 magnetometer) measure the environmental magnetic field. The activity measured at those reference sensors is used to cancel environmental noise contamination of the brain-MEG-signal. (Robinson, 1989) A LCD-projector (model DLA-G150CL, Covilex GmbH, Magdeburg, Germany) placed outside the chamber, projected stimuli via an opening in the wall on a semi-transparent screen inside the chamber (Covilex GmbH, Magdeburg, Germany). The stimulus sequence was written in and presented with the Presentation program (Version 5.5, Neurobehavioral Systems Inc., Albany, CA, USA). The viewing distance was 1.0 m. With a LUMItouch Response System (Photon Control Inc., Burnaby, DC, Canada) button presses of the right index and middle finger were recorded. Stimulation-event codes, button presses and eye movements were registered simultaneously. Eye movements were recorded with a horizontal and vertical electrooculogram (EOG) using bipolar electrode placements at the temples (horizontal), as well as a unipolar electrode below the left eye (vertical). Impedances of the Ag/AgCl-electrodes were kept below 5 kΩ (EEG-cap and Abralyt light gel, Easycap, Herrsching, Germany) and EOG-signals were amplified with an EPA-6 amplifier (Sensorium, Inc., Charlotte, VT, USA). The MEG and EOG signals were filtered online from direct current (DC) to 50 Hz low-pass and 0.01 Hz high-pass and digitized with a sampling rate of 254.31 Hz. Artifacts due to sweating (very slow potential changes) or muscle artifacts (> 100 Hz) were largely eliminated with these filters. Further artifact rejection was performed off-line. In addition central fixation was continuously monitored using a zoom-lens infrared camera mounted inside the MEG chamber.

To co-register anatomical and functional data, three anatomical landmarks (nasion and left and right preauricular points) were digitized with a Polhemus 3Space Fastrak system (Polhemus Inc., Colchester, VT, USA). These landmarks were then brought into reference with magnetic marker fields generated by five coils on defined positions on the EEG-cap (Easycap, Herrsching, Germany) all subjects wore. After repeated digitalization, i.e. registration of landmark positions on the head, the total deviance had to be smaller than 0.30 cm. A “coil-measurement” before and after each MEG recording session registered small position changes of the subject´s head, which may occur during a session and should not exceed certain limits.

3.2.4 Data Analysis

Primary MEG data analysis included off-line artifact rejection applied to epochs of interest with peak-to-peak amplitudes exceeding a threshold of 2.0 to 3.0 x10 pT. Epochs containing peak-to-peak EOG amplitudes exceeding 100 to 150 µV (depending on individual data quality) were considered to contain eye movement artifacts - blinks or leaving fixation – and were excluded from further analysis. This resulted in an average rejection rate of 18.0% for Experiment 1, 13.2% for Experiment 2, and 21,4% for Experiment 3, with no significant difference between experimental conditions. (Software: magnetic source imaging; Biomagnetic Technologies Inc., San Diego, CA, USA)

For subsequent data analysis and visualization the event-related potential software ERPSS (Event-Related Potential Laboratory, University of California, San Diego, La Jolla, CA, USA)) was used. Following artifact rejection epochs of interest, ranging from 200 ms before (baseline) to 750 ms after stimulus-onset, were extracted for each subject and averaged according to relevant experimental conditions. Furthermore, incorrect button-presses were eliminated from the data. Averages represented collapses over the different colors and were computed relative to a 200-ms-pre-stimulus baseline.

For Experiment 1, averages were computed as a function of the reward-color location in the search frames (present or absent in non-target VF) and the three different probe categories (target, reward, control) in the left and right VF, thereby collapsing data across the different colors. For Experiment 2 the same averages were computed, but separately for high- and low-reward condition, respectively, after collapsing the data of both experimental sessions for every subject. In Experiment 3 all non-rewarded arrays were analyzed according to the four distractor categories (target, reward, target and reward, control). Colors were also counterbalanced. Neuromagnetic responses to rewarded trials were not analyzed, because the signal-to-noise-ratio of those trials was too low to allow comparability with the unrewarded trials. Furthermore, the comparison between conditions is limited as there were no rewarded T&R-trials.

The *statistical validation* of waveform-differences was performed using a repeated measures analysis of variance (rANOVA) approach. If necessary, violations of data-sphericity were corrected (Greenhouse-Geisser epsilon). Respective data were reported with the original degrees of freedom, but with an adjusted level of significance (p-value). The statistical validation of onset latency differences was performed using a sliding t-test approach applied to subsequent time samples (window width of 20 msec; Guthrie and Buchwald, 1991). The first sample showing a significant difference in a sequence of at least thee subsequently significant time samples was taken to mark the onset latency.

Current source localization based on the co-registration of anatomical and functional data (see previous section). The sources of the ERMFs were then localized with a distributed source model using the minimum norm least squares (MNLS) approach with the Laplacian-weighted minimum norm, which provides the mathematical basis for the standardized low-resolution electromagnetic tomographic analysis (sLORETA) as implemented in the multimodal software CURRY 6.0 and CURRY 7.1 (Compumedics Neuroscan, Charlotte, NC, USA) (Fuchs et al., 1999). Current source estimates (CSD) for the grand-average data can be visualized in a 3-D-surface distribution. Therefore the CSD-distribution is overlaid onto a 3-D-surface segmentation of the cortical grey-matter layer of the MNI-brain, which serves as source compartment for the computation (Fuchs et al., 1998). Before averaging magnetic waveforms across subjects, the sensor array of each subject was brought into register with a reference sensor set (selected from 1500 recording sessions) representing the most canonical positioning of the sensor array relative to the anatomical landmarks. The grand average sensor data for each subject were then brought into reference with the anatomical data of the MNI brain (Montreal Neurological Institute). The standard MNI brain is a realistic anatomical model based on 152 averaged MRI T1-weighted stereotaxic volumes (used as standard template of the International Consortium for Brain Mapping (ICBM)). Specifically, first the MNI brain served as standard to create a lead field for every subject. Afterwards the inverted individual lead field was combined with the MNI-based lead field for the reference sensor set to re-compute the field distributions (using a MNLS representation of the data) as if measured with this reference sensor set.

3.2.5 Behavioral Data Analysis

To evaluate the effect of the different probe conditions on behavior (response time and percentages of correct responses) in Experiment 1 and 2, the amount of exogenous cuing entailed by the different probe-types was examined indexing the power of the probes to capture spatial attention. To this end, visual search part performance was analyzed as a function of whether the probe appeared in the VF of the target sphere (valid probe) versus in the opposite VF (invalid probe) as illustrated in Figure 12.

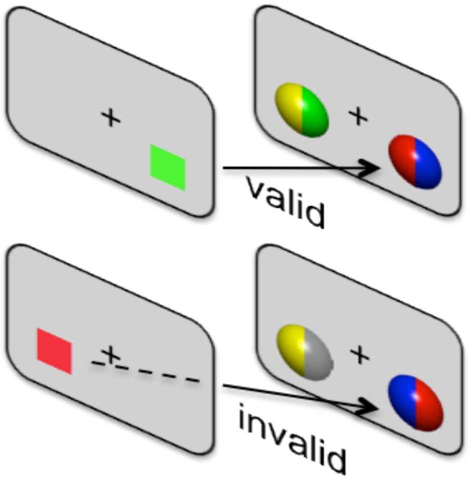

Figure 12: Example for a valid (above) and an invalid search-trial. A valid probe appeared on the same side of the VF like the subsequent target and an invalid probe on the opposite side, respective.

Given that the probe-target stimulus-onset asynchrony (SOA) varied between 600 and 900 ms (see Figure 9, ISI), the expected cuing effect is one of inhibition of return (Posner and Cohen, 1984, Klein, 2000), that is, a relative slowing of the response for valid relative to invalid probes.

All data were analyzed with MATLAB (Version 7.4, MathWorks Inc., Natick, MA, USA) and statistically validated with SPSS (Version 11.5, SPSS Inc. (IBM), Chicago, IL, USA). rANOVA and T-Test on Response time and accuracy in all Experiments were also computed with SPSS.

3.2.6 Subjects

All experiments were undertaken with the understanding and written consent of the subjects. All subjects were right-handed, had normal color vision and normal or corrected-to-normal visual acuity. They were tested for MEG compatibility in advance, so that no artifacts due to metallic implants or heart artifacts could compromise data acquisition. Subjects were paid for participation and received additional payment based on their performance in the rewarded trials. Monetary reward from every trial and every block was added up in the end and paid together with the money for participation. All experiments were approved by the ethics review board of the Otto-von-Guericke University Magdeburg.

3.3 Experiments – Quantitative Facts

3.3.1 Experiment 1

Twenty subjects (mean age 26.1 years, age range: 21 – 32, 14 females) participated in the first experiment. The payoff for rewarded trials was 5 Eurocent per trial and ranged from 10.70 to 12.00 € in total. To consider all possible combinations of color assignment to the probes, including the different control-colors and their positions, the experiment had to be divided into version A and B to avoid session durations exceeding one hour. Twelve of 20 subjects carried out version A and eight carried out version B. Each block consisted of 36 sphere- and 18 probe-stimulus presentations, yielding at 720 sphere stimuli and 360 probe stimuli in total and 60 probe stimuli for every condition (6 conditions: reward, target, control; for left and right visual field, respectively) per subject after 20 blocks.

For the analysis of the MEG responses to the search frames only the non-rewarded search frames could be taken into consideration. These 480 sphere-stimulus presentations were split into four conditions (reward present in RVF, reward present in LVF, reward absent in RVF, reward absent in LVF) with 120 stimulus presentations each for the unattended distractor stimuli.

3.3.2 Experiment 2

16 subjects (mean age 26.5 years, age range: 23 – 31, 14 females) participated in the second experiment. The payoff for rewarded trials per session ranged from 15.85 to 18.00 €. Stimuli and stimulus presentation were identical to Experiment 1. However, the experiment consisted of high- and low-reward blocks. For the former the amount of reward to be gained on a rewarded trial was doubled (10 Cent) in comparison to the low-reward blocks where subjects were rewarded with 5 Cent (same as in Experiment 1). This modification doubled the number of probe conditions as summarized in Figure 13.

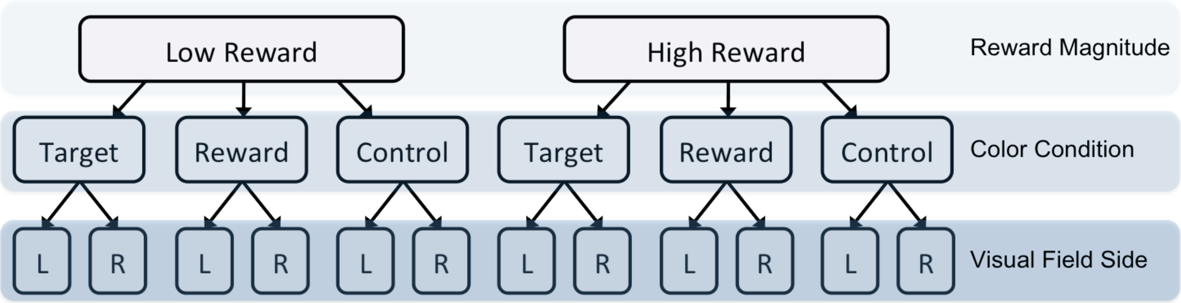

Figure 13: Probe-stimulus conditions in Experiment 2. L and R stand for left and right VF yielding in 12 possible probe-conditions in total.

Low-reward blocks and high-reward blocks alternated in an experimental session (for the different color-assignment in blocks see Figure 7 b). The doubling of experimental conditions means 40 blocks instead of 20 like in Experiment 1. Besides the remaining two versions A and B the experiment was subdivided into another two scenario versions. Inset (a) all uneven block numbers were high reward blocks, in set (b) all even numbers were high reward blocks. Subjects were told together with the color instruction before each block whether it was a high or a low reward block. All subjects had to perform two experimental sessions (on different days) with set (a) and (b), so that all blocks had been associated once with high and with low reward. As mentioned before, all other experimental conditions were kept the same. Experiment 1 already consisted of two sets, following the logic above Experiment 2 needed to have four versions: (1a), (1b) and (2a), (2b). A given subject performed set (a) and (b) either of version (1) or (2). Version (1) and (2) together guaranteed that all control-color combinations were used in equal proportion. Versions (1) and (2) were distributed equally between subjects (8 subjects performed version (1), 8 subjects performed version (2)).

After two sessions of the second experiment, 60 probe stimuli for all 12 conditions were presented to every subject, yielding at total of 360 probe-stimuli for the low-reward condition and 360 probe-stimuli for the high-reward condition.

For the analysis of the MEG responses to the non-rewarded search frames 960 sphere-stimulus presentations were split into two times four distractor-stimuli conditions as follows:

Low reward: reward present (RVF), reward present (LVF),
reward absent (RVF), reward absent (LVF);
High reward: reward present (RVF), reward present (LVF),
reward absent (RVF), reward absent (LVF).

Like in Experiment 1 this means 120 stimulus presentations for every condition.

3.3.3 Experiment 3

18 subjects (mean age 26.2 years, age range: 22 – 32, 14 females) participated in Experiment 3. The payoff for rewarded trials was 5 Eurocent and ranged per session from 14.35 to 15.95 €. Subjects had to perform 20 blocks with the duration of 3 minutes and with the same color assignment as Experiment 1 and 2 (see Figure 7 b), but without attention capturing color probes.

Each block consisted of 16 rewarded arrays and 48 non-rewarded arrays, yielding at 320 rewarded trials and 960 non-rewarded trials. Out of the 960 *non-rewarded trials* the four to be analyzed conditions as explained in section 3.2.2 and Figure 10 (control, target, reward and target + reward) in left VF had 240 sphere-stimulus presentations each per subject.

To limit the number of *rewarded trials* to 25% of all stimuli only three conditions of distractor stimuli in the unattended LVF were shown. Two third were control-condition, and one third were target and reward condition, respectively. In order to avoid confusing the subjects with two target + reward spheres together in one search frame the theoretically possible target + reward condition has been omitted for rewarded trials.

4 Results

The results of Experiment 1 and Experiment 2 are reported in Buschschulte et al. (2014) and the results of Experiment 3 in Hopf and colleagues (2015). In this section the results for attentional-capture part and for the visual search part of the same experiments are presented separately.

4.1 Experiment 1

4.1.1 Contingent Attentional Capture Part of Experiment 1

4.1.1.1 Behavioral Performance as a Function of Probe Color and Probe Location (Experiment 1)

Subjects were to ignore the probes, so that no direct behavioral data reflecting stimulus feature processing is available. Nevertheless, probes were designed to capture spatial attention and would therefore impart an exogenous spatial cuing effect on performance in the subsequent task-relevant search frame (Posner, 1980). Specifically, the appearance of the probe and the target in the same versus the opposite VF is named “valid” versus ”invalid”, respectively (see section 3.2.5). As the probe-target SOA (see ISI in Figure 9) varied between 650 and 950ms, the expected cuing effect would be inhibition of return (IOR), i.e. a performance decrement, for validly cued targets. Note that faster responses typically seen after valid cues are only obtained for much shorter SOA (<250 ms) (Klein, 2000). Taken together, the amount of cuing elicited by the different probe types will provide an index of the degree to which spatial attention was captured.

Figure 14 a shows the IOR-effect in response time for the valid relative to the invalid conditions. On average valid probes lead to an 11 ms slower response than invalid probes. Consistently, a two-way rANOVA with the factors probe validity (valid/invalid) and probe condition (target, reward, control) yielded a significant main effect for probe validity (F(1,19)=19.9; p<0.0001), but no probe validity x probe condition interaction (F(2,38)=0.66; p=0.57).

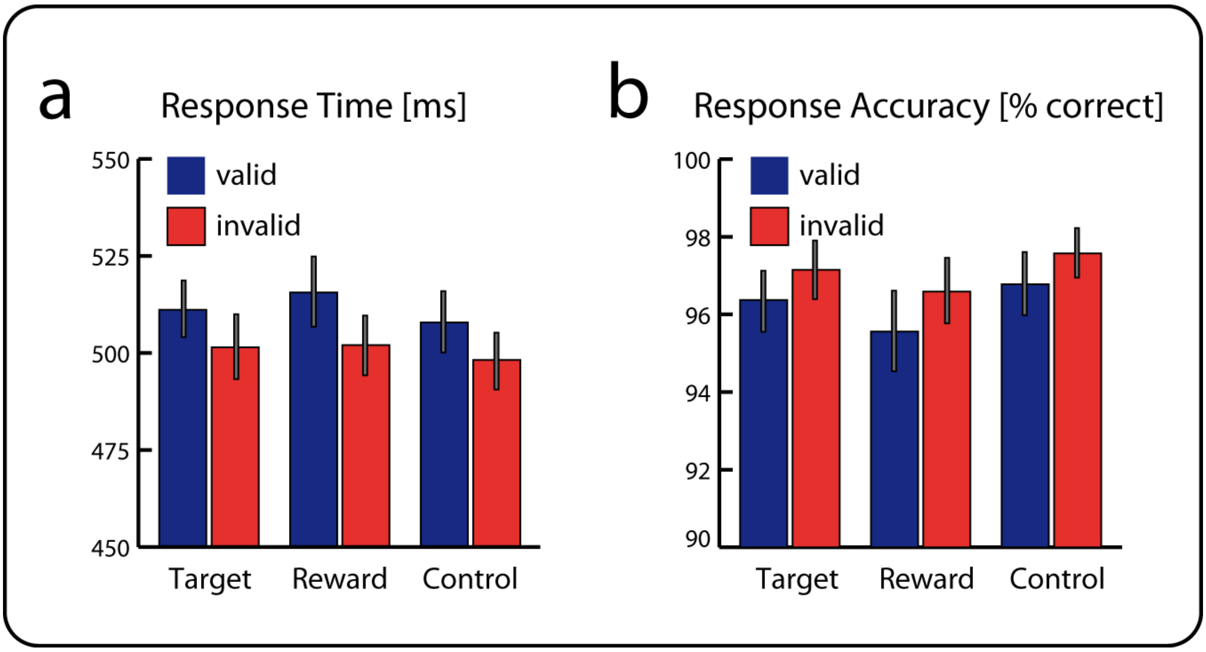

Figure 14: Task-performance as a function of probe-location for Experiment 1. On the left hand side mean response times (a) and on the right hand side accuracy (b) averaged over all 20 subjects is displayed. The conditions target, reward and control refer to the color of the probe, shown prior to the search task arrays. For every probe condition the exogenous cuing effect is visible in the comparison of the valid (blue bars) and invalid (red bars) condition. Probes presented in the same VF as the target are valid probes, while probes presented in the opposite VF are invalid. The vertical white bars on top index the standard error of mean for every condition.

Post-hoc T-tests comparing validity within probe conditions showed significant differences between valid an invalid probes for target (t (1,19)=2.64; p<0.05), reward (t(1,19)=4.06; p<0.005), and control (t(1,19)=2.82; p<0.05). There was a small difference in RT between probe conditions, but the main effect of probe condition did not reach significance (F(2,38)=2.76; p=0.09). RTs were slightly slower for targets following reward-probes compared to target or control-probes.

Figure 14 b illustrates the effect of probe validity with respect to the accuracy measures (%-correct responses). Response accuracy (RA) was significantly higher for valid than for invalid probes as the respective rANOVA shows (F(1,19)=4.87; p<0.05) supporting the idea of a general attention capturing effect of the probes. But no interaction of probe validity with probe condition could be observed for RA (F(2,38)=0.03; p=1.0).

Like for RT there was a trend toward a main effect of probe condition for performance accuracy (F(2,38)=2,83; p=0.08), indicating that accuracy was slightly reduced for targets after reward-probes relative to target and control-probes.

Having in mind that the overall IOR effect is rather small and the effect of probe condition is not significant for RA and RT, however, the general response pattern should be taken just as a hint at a reward effect for performance (slightly increased IOR effect), which of course cannot be guarantied with these data.

In general the small, but significant IOR-effect for valid probes validates the presence of an attentional capture effect which is a prerequisite for further ERMF-analysis of the probes in their respective color conditions.

4.1.1.2 MEG Responses to the Color Probes (Experiment 1)

ERMF waveforms and respective field distributions of probe color conditions (target, reward, control) are shown in Figure 15. The waveforms of Figure 15 a on the left were recorded at selected sensor sites, which are marked with arrows over the left and right occipito-temporal cortex contralateral to the VF of probe presentation in the respective topomaps on the right. Waveforms and topomaps for probes in the RVF are depicted in the upper row, for probes in left VF in the lower row. Target-probes (red traces) showed an enhanced neuromagnetic response at ~180-280 ms after probe-onset relative to control-probes (black traces). Reward-probes (green traces) elicited no enhanced amplitude, and their response remained almost indistinguishable from control-probe-waveforms.

The topomaps on the right (Figure 15 a) show the average ERMF response between 180 and 280 ms for the three probe conditions. The influx-efflux configuration for the activation contralateral to the presentation of the probe stimulus is marked with black ellipses over the lateral occipito-temporal cortex. (See also section 3.1 “Magnetoencephalography Basics” and Figure 5) A high density of black contour lines in an influx-efflux transition zone suggest a strong underlying current source. Efflux and influx components together form the magnetic field that is generated by source activity as shown in Figure 15 b. The source is located under the transition zone between both components marked with an asterisk in Figure 15 a. Enhanced waveform amplitudes correspond with deeper blue and red colors in the topomaps.

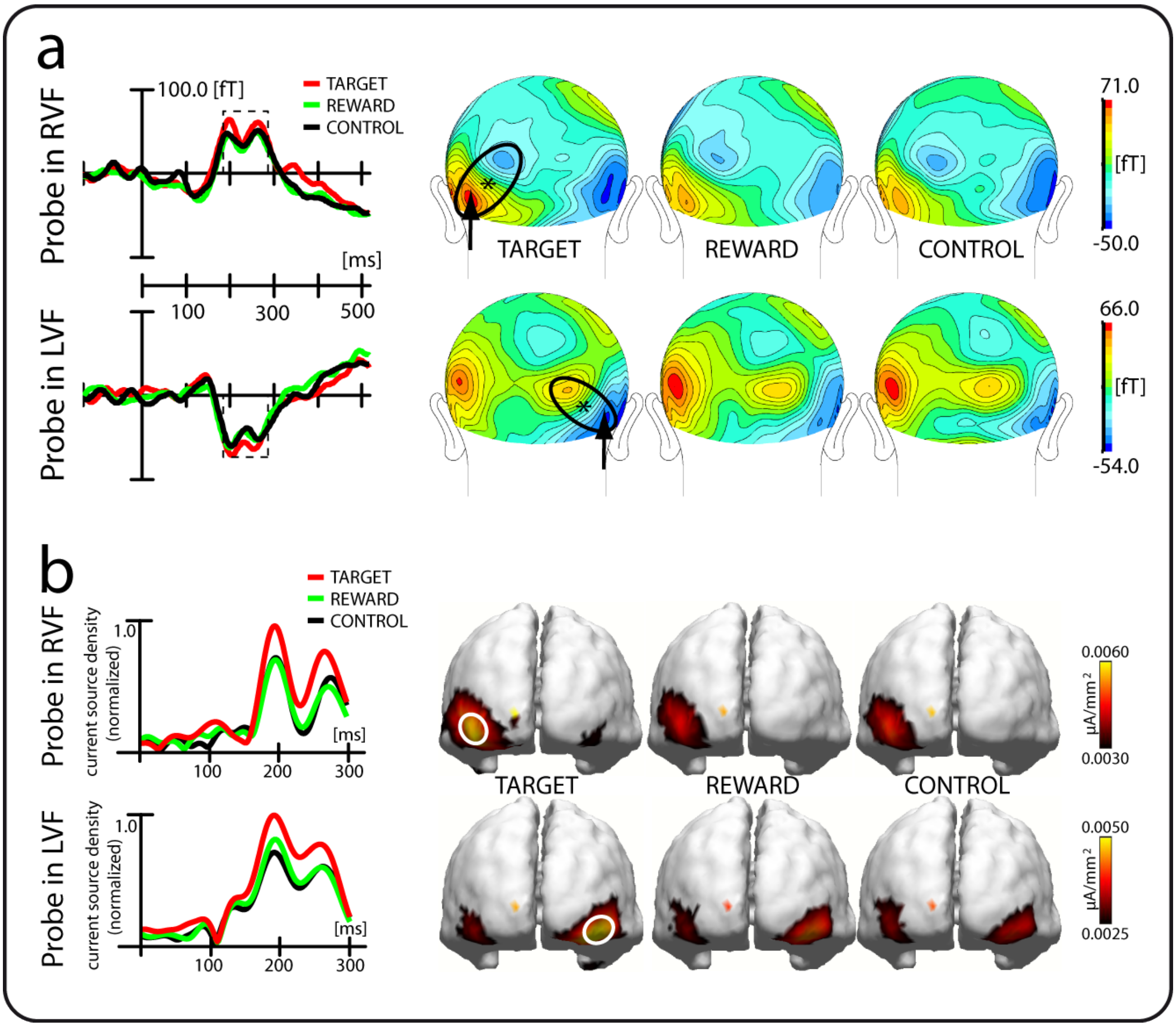

Figure 15: MEG responses to color probes of Experiment 1. (a) On the left: ERMF-waveforms elicited by probes in target (red), reward (green) and control-color (black). Notice, that the colors are only used for demonstration and do not represent stimulus colors! Waveforms are averaged over 20 subjects and recorded at the sensor sites indicated by small arrows contralateral to the VF of probe presentation (right VF: upper row, left VF: lower row). On the right: Magnetic field distributions (topomaps) for mentioned conditions. The response to the probes is represented by an influx-efflux field configuration, which is marked with black ellipses. The probable location of the underlying source in the transition zone between influx and efflux is marked with an asterisk. (b) Corresponding source-waveforms (right) and current source density (CSD) distributions (left). The source waveforms represent time-course of source density estimates at a certain location and are normalized. The respective cortical regions centered at the source density maximum are highlighted with small white circles. The CSD distributions in (b) confirm the source localization of the influx-efflux configuration in (a).

The difference in response strength is also visible here, because a stronger field effect for target-probes relative to reward and control-probes can be seen, with the latter two showing effects of comparable size. A statistical analysis validates these observations. A three-way rANOVA with the factor probe condition (target, reward, control) was performed on the mean ERMF response between 180 and 280 ms post stimulus for probes presented in both VFs separately at respective contralateral sensor sites (arrows in Figure 15 a). In RVF the respective sensor is A196 and in LVF sensor A245. The analysis yielded a significant main effect for probe condition for both, RVF-probes (F(2,38)=5.2, $p<0.01$), and LVF probes (F(2,38)=4.66, $p<0.05$). Subsequent paired comparisons (paired-samples t-tests) confirm the visible waveform differences between probe conditions. So target-probes differed significantly from control (RVF probes: p=0.0048, LVF probes: p=0.014) and reward-probes (RVF probes: p=0.0018, LVF probes: p=0.041), while reward and control-probes did not differ (RVF probes: p=0.68, LVF probes: p=0.29).

To localize the ERMF effects shown in Figure 15 a the current source density (CSD) analysis was performed on the neuromagnetic responses to the three probe-types in both VFs. The results in μA per mm^2 are shown in Figure 15 b for probes in RVF in the upper row and for probes in LVF in the lower row. The CSD-distribution (MNLS estimates, see methods section) was visualized in the six topographical maps on the right hand side. The distribution was overlaid onto a 3-D surface segmentation of the cortical grey matter layer on the MNI-brain. Stimulation in left and right VF did not result in exactly mirrored ERMFs or exact same sources, but qualitatively similar response patterns. Effects between probe conditions were more prominent for probes in right VF. In line with the field distributions in Figure 15 a the estimated CSD strength was maximal for target-probes, while reward and control-probes elicited comparable but smaller effect sizes on both sides of presentation. Maxima of all three probe-types appear in similar regions of the inferior occipito-temporal cortex contralateral to the VF of stimulus presentation.

On the left hand side of Figure 15 b this is further illustrated by the time-course of CSD-estimates obtained from regions of interest (ROIs, white circles) at the CSD-maximum for all three probe conditions. The CSD of target-probes (red) increased beyond that of reward (green) and control-probes (black), starting at about 180 ms after probe onset and lasting till about 280 ms.

In summary, the comparison of the ERMF waveforms as well as the underlying current source density distribution of the three probe-types revealed that reward-probes elicited a response in ventral extrastriate cortex roughly indistinguishable from control-probes, suggesting that a reward-relevant feature, which is not task-relevant, does not automatically entail modulatory effects in visual cortex. In contrast, the color of the target-probe, which was relevant for subsequent target performance, produced a significantly enhanced activity in extrastriate visual cortex.

4.1.2 Color Search Part of Experiment 1

4.1.2.1 Behavioral Performance as a Function of Reward-Color Location (Experiment 1)

In contrast to the results to probe stimuli reported in the previous section, for the search task direct behavioral data was available. In Figure 16 the response time (a) and response accuracy (b) measures in Experiment 1 are summarized as a function of where the reward-color was presented in the search frames. In rewarded trials reward-color was present in the target. In non-rewarded trials the reward-color could only be present in the opposite distractor sphere, while subjects were asked to ignore it in in favor of proper target-color discrimination. In one third of the search frames the reward-color was absent, because in these non-rewarded trials the distractor sphere contained two control-colors.

Interestingly, when the reward-color appeared in the distractor sphere RT (Figure 16 a) was slowed relative to when it was combined with the target (rewarded trial) or was absent. This finding could be validated with a three-level factor rANOVA for reward location (in target, in distractor, absent) by showing a significant effect ($F(2,38)=30.7$; $p<0.0001$). Post hoc pairwise comparisons confirmed this effect of decreased reaction time for the reward-color appearing in the distractor relative to the other conditions (reward-color in target versus in distractor: $p<0.0001$; reward-color absent versus in distractor: $p<0.0001$). Notably, subjects did not respond faster to rewarded trials with the combination of both, the reward- and the target-color in one sphere than for reward-color absent trials ($p=0.112$).

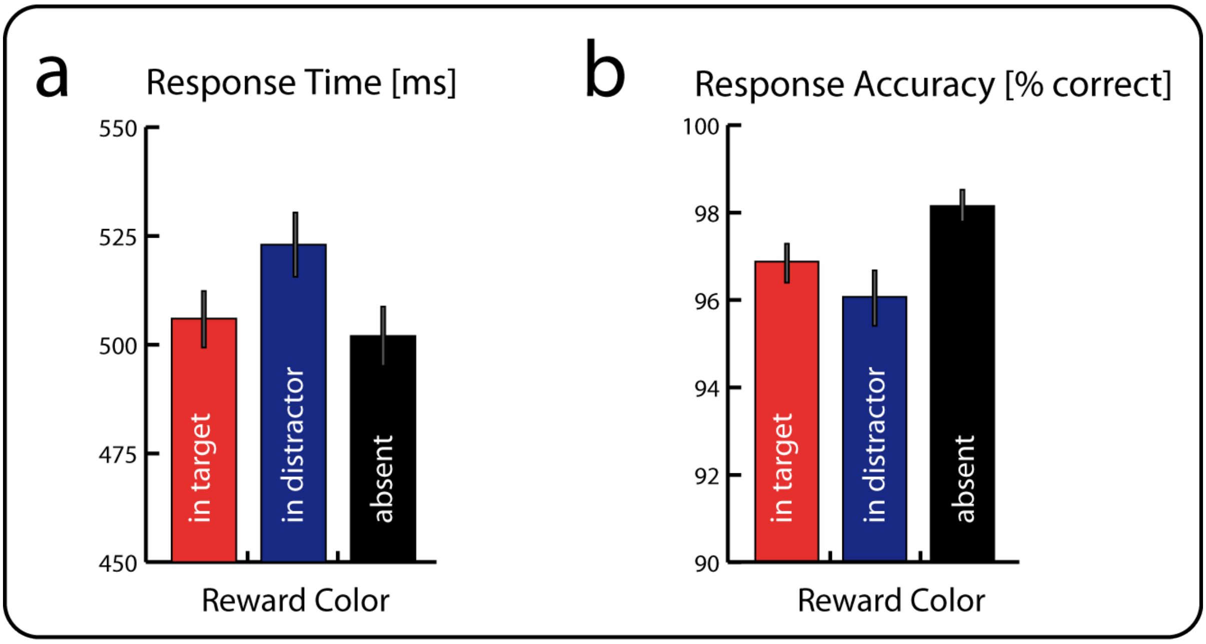

Figure 16: Behavioral performance data of the search task of Experiment 1 in respect to reward-color location. All Data were averaged over the 20 subjects of Experiment 1. The "in target" condition (red bar) refers to target and reward-color together in one sphere, "in distractor" condition (blue bar) to the reward-color in the opposite sphere to the target and "absent" condition (black bar) means that no reward-color appeared on the screen. Response times (a) are shown on the left and accuracy (b) on the right. Slowest response times and decreased accuracy can be seen for the "in distractor" condition. The vertical grey bars on top of the big bars index the standard error of mean for every condition.

Reward-color did also influence response accuracy in percentage correct responses (Figure 16 b) in a significant way. A respective rANOVA yielded a significant result (F(2,38)=11.3; p<0.005). While accuracy was generally high, subjects were more prone to errors with the reward-color present on the screen than in reward-color absent trials. This was confirmed with post hoc pairwise comparisons showing that reward-color absent trials yielded in higher accuracy than when the reward-color was combined with the target (p<0.005), or within the distractor (p<0.0001). Subjects performed also more accurate when the reward-color was part of the target-sphere than when it appeared in the distractor, but this effect was not significant (p=0.102).

Theoretically, a subject could have just concentrated on the target, disregard the reward-color and would have been able to perform the task equally well. This is not the case.

While the focus of attention was directed to the VF containing the target sphere, the reward-color presented in the opposite VF apparently seemed to be salient and therefore distracting. The best performance was observed for target-only trials where no reward appeared and competed for cognitive resources. In sum, these behavioral data indicate that during the search task the reward-relevant color feature influenced stimulus-processing resulting in decreased performance for reward-stimuli.

4.1.2.2 MEG Responses to the Search Frames (Spheres) (Experiment 1)

The MEG response to color probes showed an increased response to probes drawn in the task-relevant target-color, but not for reward-associated or control-probes. However, the analysis of the ERMF-response to the search frames investigates whether a similar picture can be observed for respective colors in the unattended distractor sphere during the search task. As the target-color was never present in the distractor sphere, only the reward-color could be compared with the control-colors in the distractor sphere.

Figure 17 below shows waveforms elicited by the sphere-stimuli of the non-rewarded trials. Green traces reflect the response to distractor spheres containing the reward-color, whereas black traces represent the response to the control-colored distractor in the absence of reward. These waveforms were recorded from a selected sensor site showing the maximum modulatory effect over the hemisphere contralateral to the unattended VF of distractor presentation. Apparently, the reward-color causes a response enhancement relative to the control in the second waveform deflection starting around 200 ms after search frame onset.

For each VF rANOVAs with the factor reward-color (present/absent in non-target VF) on mean amplitude measures between 200-280 ms confirm this finding by yielding significant effects for the RVF ($F(1,19)=10.09$, $p<0.005$) as well as the LVF ($F(1,19)=8.3$, $p<0.01$).

The topographical maps displayed above the respective waveforms in Figure 17 show the results of the current source localization analysis, which was based on the ERMF difference between the reward-color present minus absent condition. The current source maxima can be observed over ventral lateral extrastriate visual cortex, contralateral to the side of reward-color presentation.

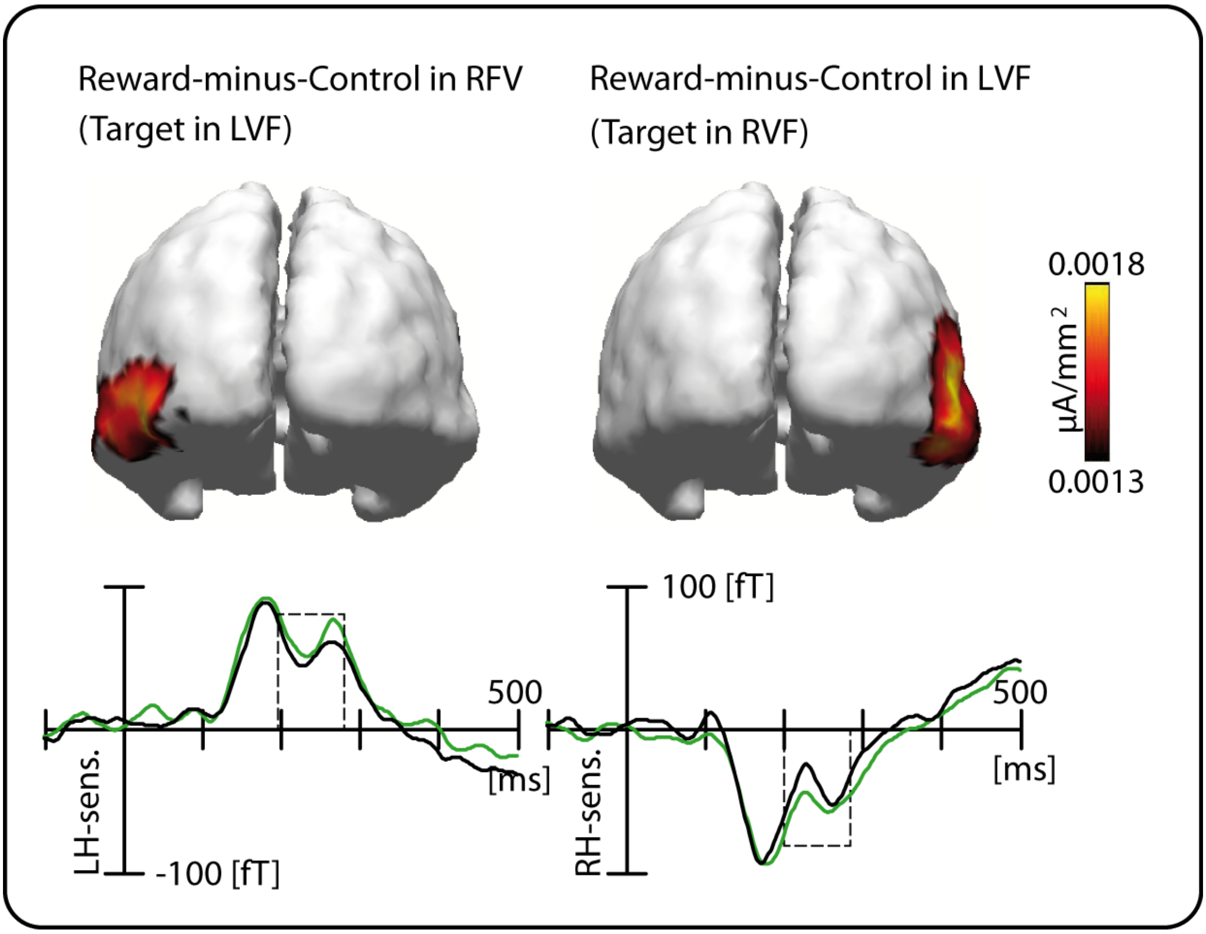

Figure 17: MEG responses to search frames of Experiment 1. ERMF waveforms were elicited by non-rewarded search frames, with the reward-color being present (green waveforms) or absent (black waveforms) measured contralateral to the VF of distractor presentation. Respective sensors over the left and right visual hemifield are marked with RH-/LH-sensor. The topographical maps in the upper row show the corresponding CSD distributions in a dark red to light yellow scale estimated for the reward-minus-control difference. Current source maxima can be seen over the contralateral extrastriate cortex.

Confirming the behavioral observations (search task) the reward-color led to a response modulation. While the ERMF responses to task-irrelevant reward-probes had no modulatory effect on extrastriate processing, an enhancement was seen when subjects performed the task. Hence, reward-relevance did in fact bias color feature processing, but respective bias is only revealed when subjects actually perform the visual search task.

4.2 Experiment 2

4.2.1 Contingent Attentional Capture Part of Experiment 2

The first experiment revealed, that there is a bias in extrastriate cortex for a color feature associated with reward during visual search. In contrast, it seems that involuntary orienting was not influenced by the reward-color when presented in a task-irrelevant color probe. Hence, it is the possible that modulatory effects to reward were absent because the reward size was not significant enough. To test this possibility, two levels of monetary reward were introduced in Experiment 2. First, the experiment was run in blocks with moderate reward level (5 Euro-Cent), which was the same as in Experiment 1 (low-reward trials). Second, we run blocks where the amount of reward was doubled (10 Euro-Cent). Subjects performed alternating high- and low-reward blocks. Besides the change in to be gained reward, stimulation, trial structure, and experimental task remained identical to Experiment 1 (see methods section for details).

4.2.1.1 Behavioral Performance as a Function of Probe Color and Probe Location (Experiment 2)

As in Experiment 1 an IOR effect for valid versus invalid probes could be observed for Experiment 2. Figure 18 a illustrates that valid probes following the target sphere in the same VF lead to slower response times than invalid probes, which follow in the opposite VF of target presentation. RT was also generally faster under high-reward condition than under low-reward condition. For probe validity a three-way rANOVA with the factors validity (valid/invalid), probe condition (target, reward, control), and reward size (low, high) confirmed significant main effects (F(1,15)=43.2; p<0.0001). The main effect for reward size (F(1,15)=13.8; p<0.005) was also significant, in contrast to the main effect of probe condition (F (2,30)=1.1; p<0.4). The interactions of reward size x probe condition (F(2,30)=1.4; p<0.3), probe validity x probe condition (F(2,30)=2.0; p<0.15), reward size x probe validity (F(1,15)=0.54, p<0.5) were not significant.

Accuracy (Figure 18 b) is with over 96% higher than in the first experiment. But accuracy reveals only minimal variation with experimental conditions, without any systematic effect of probe validity, probe condition or reward size. Consistently a respective rANOVA reveals that neither of the respective main effects was significant, i.e. probe validity ($F(1,15)=0.29$, $p<0.6$), probe condition ($F(2,30)=1.03$ $p<0.4$), and reward size ($F(1,15)=0.49$, $p<0.5$).

In sum, probe condition had no systematic effect on cuing, but the IOR-effect observed for Experiment 1 is also true for response times in Experiment 2.

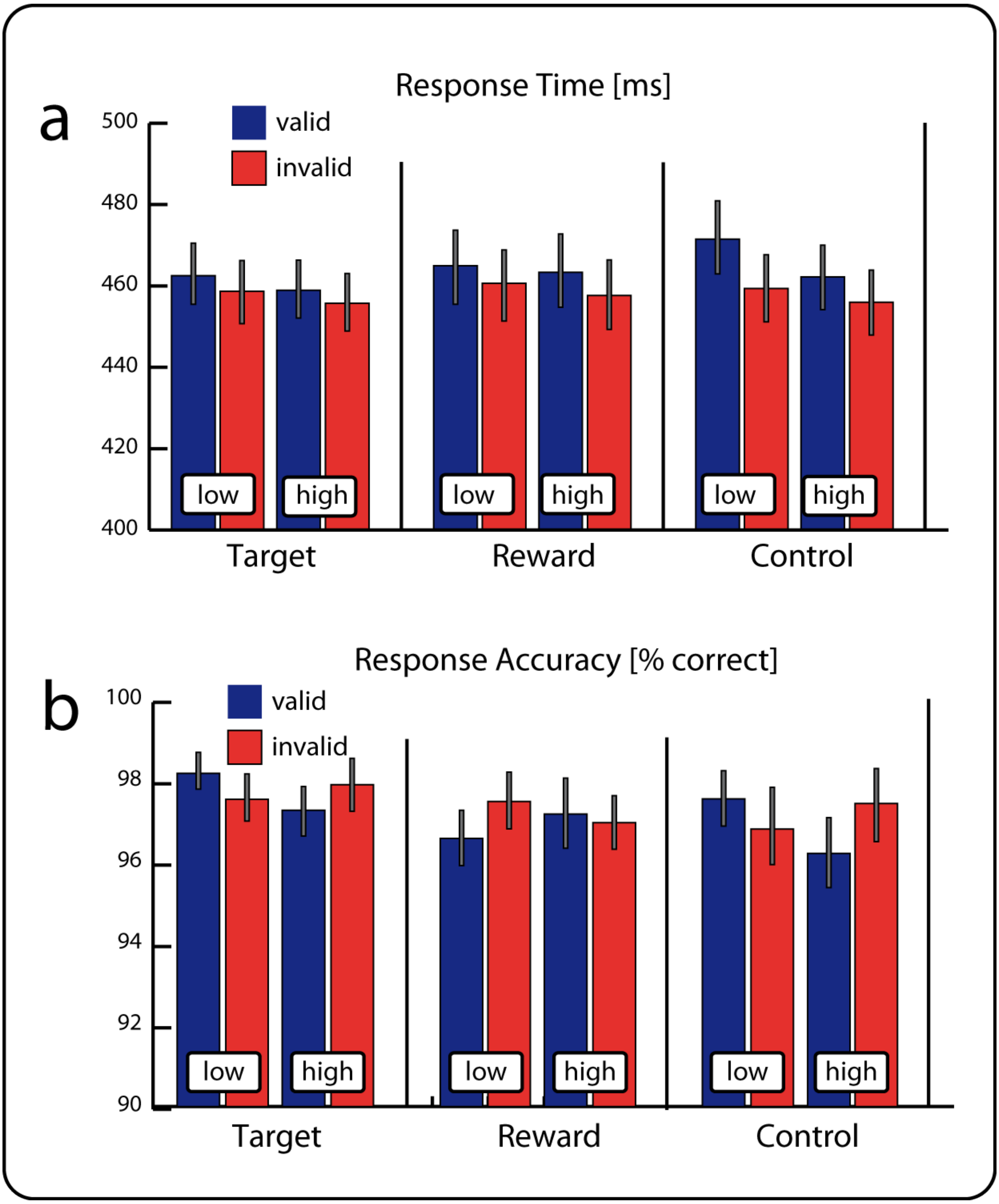

Figure 18: Task-performance as a function of probe-location for Experiment 2. Shown are mean response times (a) and percent correct (accuracy) (b) values for targets following color probes in the same VF as the probe (valid, blue bars) or in the opposite VF (invalid, red bars). Averaged data over 16 subjects are shown separately for probes drawn in the target-color (target), the reward-color (reward), and the control-color (control). Additionally for all probe conditions the low reward condition (low) and the high reward condition (high) is displayed. The vertical white bars represent the standard error of mean for every condition.

4.2.1.2 MEG Responses to the Color Probes (Experiment 2)

Figure 19 shows waveforms and ERMF distributions of target-, reward- and control-probes presented in right VF. Note that the pattern of probe-effects was smaller but qualitatively similar in the left visual hemifield. The upper row depicts the low-reward condition (a), the high-reward condition (b) is shown below.

The probes ERMF response under the low-reward condition (a) perfectly reproduced the pattern seen in the first Experiment. Target-probes (red traces) elicited an increased response in ventral extrastriate cortex between ~180-270 ms relative to reward (green traces) and control-probes (black traces), with the latter probe types being nearly indistinguishable.

Although response sizes were generally smaller the probe response pattern under the high-reward condition (b) between 190-220 ms resembles the low reward condition, i.e. higher amplitude of the target waveform and nearly undistinguishable reward and control waveforms. However a difference to the low-reward condition was visible starting at 220 ms post stimulus, where the response to reward-probes decreased relative to target and control-probes lasting until about 250 ms.

The corresponding topomaps on the right side of Figure 19 confirm these observations. They show the distribution of the mean probe-response for the three probe-types of the low-reward condition at 200 ms (a), as well as the high-reward condition at 200 ms (upper row maps in panel b) and at 230 ms (lower row maps in panel b). At 200 ms post stimulus the ERMF response to target-, reward-, and control-probes field distributions and amplitude pattern for both, low- and high-reward condition, look very similar. That is, target-probes elicited stronger field responses (black ellipses) over the left lateral occipito-temporal cortex than reward- and control-probes. This is reflected by stronger colors and more contour lines of the influx-efflux configuration in the map. The picture changed around 220 ms (lowest row) after probe-onset for the high-reward condition. Here target- and control-probes show an influx-efflux configuration of similar size, whereby the middle topomap for the reward condition shows a significantly reduced response pattern over the left lateral occipito-temporal cortex.

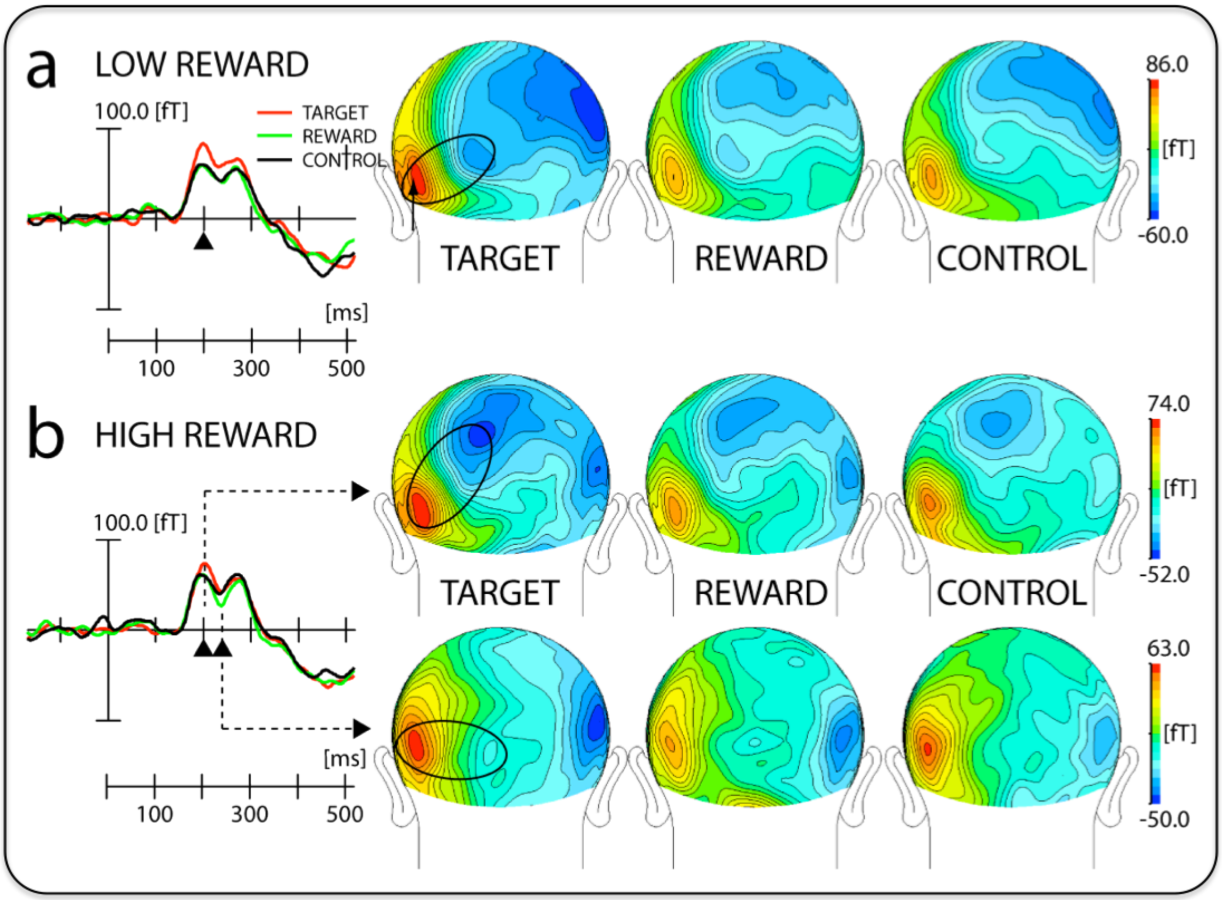

Figure 19: MEG responses to color probes of Experiment 2. Shown are waveforms and topomaps for the RVF for target- (red trace), reward- (green trace) and control-probes (black trace) under low (a) and high reward condition (b), averaged over 16 subjects. Waveforms originate from sensor sites indicated by the small arrow in (a) and correspond with the sensor site shown in Figure14 (a) for Experiment 1. The topomaps on the right hand side show the ERMF-response distribution at 200 ms after probe-onset indicated by the black arrowheads in the waveforms on the left. Under high reward conditions (b) topomaps at 200 ms and 230 ms are shown. Black ellipses highlight the influx-efflux field configuration, which represent the response to the probes.

In the time range from 190 - 220 ms and from 220 - 250 ms the ERMF-effects for the mean responses were statistically validated with a rANOVA with the factors probe-condition (target, reward, control) and reward-size (low, high). In the earlier time-range from 190 - 220 ms probe condition (F(2,30)=3.9, p<0.05; sensor A214) yielded a significant the main effect.

This validates that the response to target-probes was enhanced relative to reward and control-probes with no difference between low- and high-reward condition, because no interaction for probe condition with reward size (F(2,30)=0.69) was observed. A subsequent planned comparison confirmed the difference between target and control-probes (F(1,15)=9.45, p<0.01) with a significant effect. For reward and control-probes (F(1,15)=0.27) no effect could be observed. The main effect of reward-size (F(2,30)=7.07, p<0.05) indicates that the ERMF-responses to the probes were generally smaller under high- than under low-reward conditions. Between 220 and 250 ms, the factor probe condition showed no statistical effect (F(2,30)=0.29, sensor A214). Importantly, the interaction of probe-condition with reward-size (F(2,30)=3.7, p<0,05) was significant, which validates the attenuated response to reward-probes under high-, but not under low-reward conditions. Even though the response to the probes was smaller under high- than under low-reward condition in this later time range, the main effect of reward-size did not reach significance (F(2,30)=2.73, p=0.14).

Figure 20 shows the results of the source localization analysis performed on the mean target-minus-control differences and reward-minus-control difference temporally corresponding with the ERMF effects. Analogous to Figure 19, these source density estimates are shown for RVF probes only. On the left the target-minus-control difference between 190 and 220 ms is shown for the low-reward condition at the top and the high-reward condition at the bottom. Current sources are scaled from black to yellow and maxima are highlighted by a white and a green dot. Apparently, CSD maxima are located over the left ventral-lateral occipito-temporal cortex consistent with current source maxima in Experiment 1 (cf. Figure 15 b, upper row).

On the left of Figure 20 the reward-minus-control difference of the high-reward-condition between 220 and 240 ms is shown. The map is scaled in blue colors to highlight that the CSD distribution shows the reduced response to reward-probes relative to control-probes. The maximum of the reward-minus-control difference is marked with a red dot and also appears over the ventral occipital cortex, but at a site more posterior than the maxima of the target-minus-control differences. For better orientation the white and green dot of these maxima are also depicted in this map.

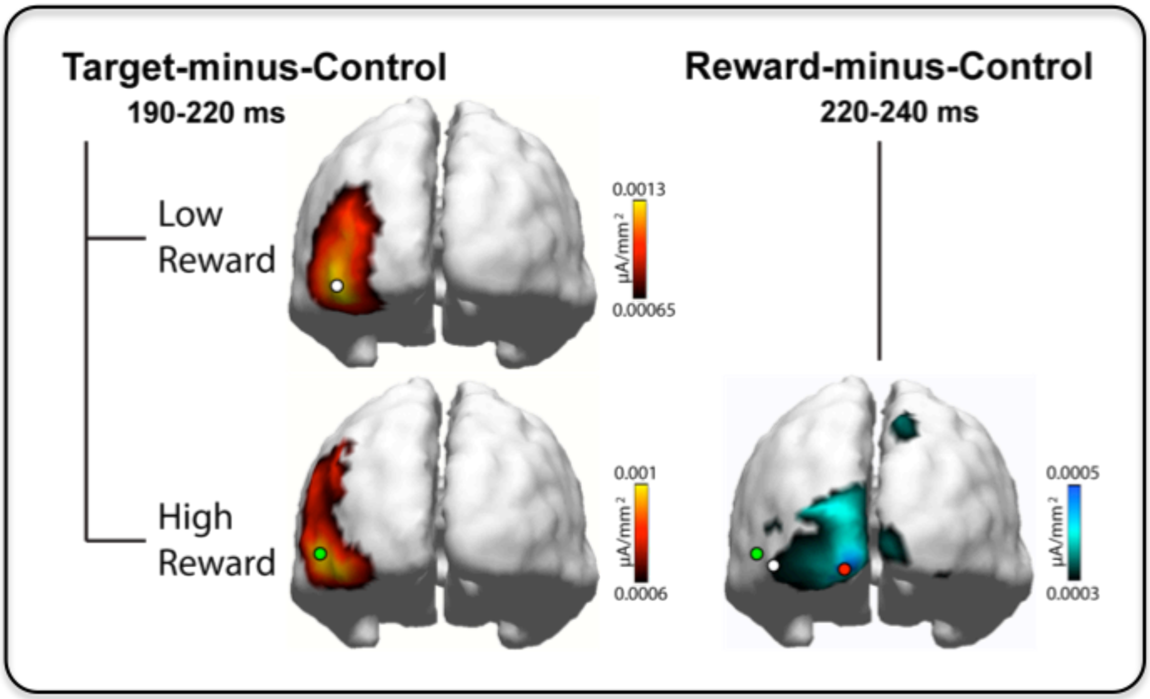

Figure 20: Current source density analysis for responses to probes in Experiment 2. Left: CSD distributions (minimum norm least square) estimated for the response difference target-probes minus control-probes (Target-minus-Control) for the low-reward condition at the top and the high-reward condition at the bottom. CSD maxima are highlighted with small dots (white, green).
Right: CSD distributions estimated for the response difference reward-probes minus control-probes (Reward-minus-Control). The CSD maximum is marked with the red dot. For comparison the maxima of the Target-minus-Control estimates are also shown (white and green dot).

To sum up briefly, the low-reward condition of Experiment 2 perfectly replicates the results of Experiment 1: The reward-relevant feature does not automatically entail modulatory effects in visual cortex. This also applies to the initial response of the high-reward condition (until 220 ms). Between 220 and 250 ms, however, the response to reward-probes was attenuated, presumably reflecting an inhibitory effect on neural processing. The attenuation effect is located at a more posterior site in ventral extrastriate cortex (Figure 20), consistent with an inhibitory modulation that serves to block forward activity at an early level of visual processing (see section 4.3 Effects to Color Probes outside the Visual Cortex for Experiment 1 and Experiment 2).

4.2.2 Color Search Part of Experiment 2

4.2.2.1 Behavioral Performance as a function of Reward-color Location in the Search Frames (Experiment 2)

Figure 21 shows response time (a) and response accuracy (b) measures of Experiment 2 as a function of the location of the reward-color in the search array. This was done separately for the low-reward condition shown on the left and high-reward condition shown on the right, respectively. The reward-color could either appear in the target-sphere (red and pink columns), in the distractor (blue columns) or could be absent (black and grey columns).

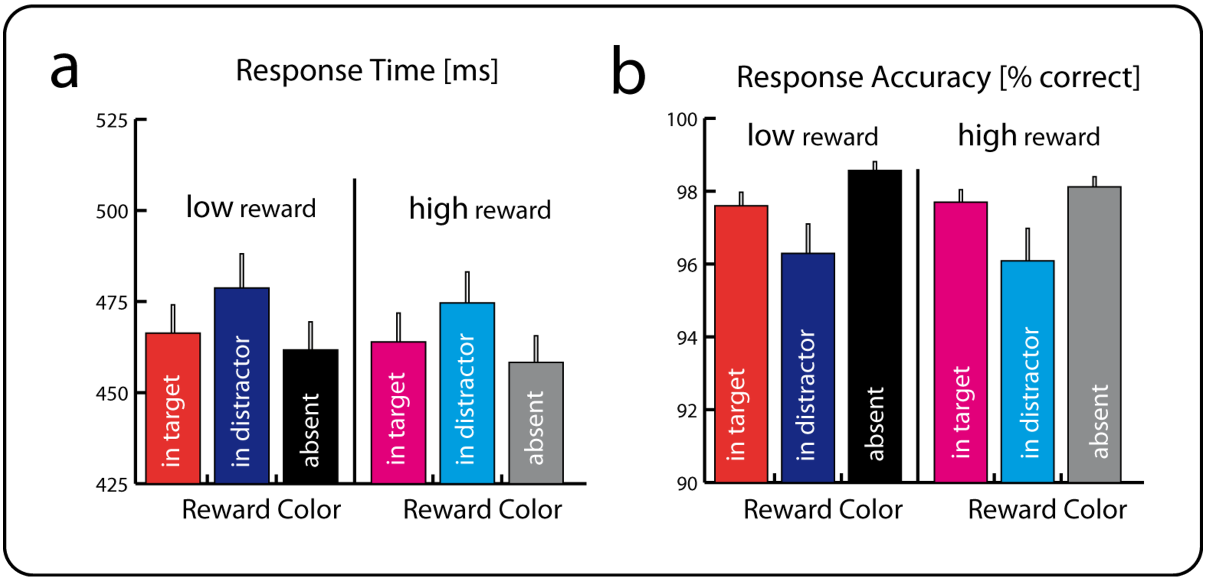

Figure 21: Behavioral performance data of the search task of Experiment 2 in respect to reward-color location. All Data were averaged over the 16 subjects of Experiment 2. The "in target" condition (red/pink bar) refers to target and reward-color together in one sphere, "in distractor" condition (blue/light blue bar) to the reward-color in the opposite sphere to the target and "absent" condition (black/grey bar) means that no reward-color appeared on the screen. Data is shown separately for the low-reward (in a and b on the left) and the high-reward (in a and b on the right) condition. Response times (a) are shown on the left and accuracy (b) on the right. Slowest response times and decreased accuracy can be seen for the "in distractor" condition under low- and high-reward condition. The vertical white bars index the standard error of mean for every condition.

Consistent with the observation in Experiment 1 (see Figure 16), RTs were slowed for the reward-in-distractor condition relative to the reward-in-target condition (rewarded trial) or when the reward-color was absent. In addition, subjects reacted slightly slower when the reward-color was presented together with target-color relative to the reward absent condition. This pattern could be observed for both the low- and high-reward condition.

A two-way rANOVA with the factors reward location (in target, in distractor, absent) and reward size (low, high) confirms these observations by showing a significant main effect of reward location (F(2,30)=23.2, $p<0.0001$), but no interaction of reward location x reward size, (F(2,30)=0.49, $p=0.58$). However, there was a significant main effect of reward size (F(1,15)=12.3, $p<0.005$), which confirms the observation that RT was generally faster under high-reward conditions. Pairwise post hoc comparisons revealed a decreased RT for the reward-in-distractor condition relative to the reward-in-target condition (F(1,15)=19.2, $p<0.005$), and the reward absent condition (F(1,15)=27.9, $p<0.0001$). Subjects were also slightly slower in the reward-in-target than in the reward-absent condition and this effect also reached significance (F(1,15)=13.6, $p<0.005$).

Together, these observations indicate that the presence of the reward-color had a generally distracting effect, which was largest when appearing in the distractor.

The response pattern for accuracy shown in Figure 21 b illustrates the distracting effect of reward as well, leading to decreased performance for the reward-in-distractor condition relative to conditions where the reward-color appeared in the target or was absent. Again, reward size did not affect this effect.

This was confirmed by a two-way rANOVA with the factors reward location (in target, in distractor, absent) and reward size (low, high) resulting in a significant main effect of reward location (F(2,30)=7.6, $p< 0.01$), without a significant interaction effect for reward location x reward size (F(2,30)=0.86, $p=0.43$). And also no main effect of reward size (F(1,15)=1.2, $p=0.29$) could be observed. Subsequent planned comparisons revealed that subjects performed worse for the reward-in-distractor condition relative to the reward-in-target condition (F(1,15)=5.5, $p<0.05$), and the reward-absent condition (F(1,15)=9.5, $p<0.01$). The small RA decrement observed for the reward-in-target condition versus the reward-absent condition was also significant (F(1,15)=6.5, $p<0.05$).

4.2.2.2 MEG Responses to the Search Frames (Spheres)

The bottom of Figure 22 shows waveforms representing non-rewarded search frames. Green traces represent the reward-color-present condition, while black traces represent the reward-color-absent condition for distractor spheres in the non-target VF. Waveforms at the top show the results for low-reward blocks and waveforms at the bottom the results for high-reward blocks. Like in Experiment 1 (compare Figure 17), the reward-color elicited an enhanced ERMF response between 200 and 260 ms after search frame onset under low-reward condition. At the top of Figure 22 the corresponding topographical CSD distributions for both visual hemifields again reveal a current source maximum in ventral extrastriate cortex contralateral to the VF of reward-color presentation. Remarkable is the finding that this modulatory effect is abolished under high-reward condition, i.e. the response to the reward-colored distractors was indistinguishable from the response to the double control-colored spheres.

For statistical validation, a two-way rANOVA with the factors reward-color in non-target VF (present/absent) and reward size (low, high) was computed on mean amplitude measures between 200 and 260 ms post stimulus. A significant main effect of reward-color ($F(1,15)=6.09$, $p<0.05$), and a significant interaction between reward-color and reward size ($F(1,15)=4.62$, $p<0.05$), but no main effect of reward size ($F(1,15)=0.08$) was observed. Post hoc pairwise comparisons yielded a significant effect of reward-color for low-reward trials ($F(1,15)=7.49$, $p<0.05$), but no such effect for high-reward trials ($F(1,15)=0.11$).

The results for the search task under low-reward condition reveal that reward-colors were not ignored and confirm the respective behavioral data for the search task. This also corresponds to the findings of Experiment 1. For the high-reward condition no such effect can be seen, as the waveforms of the reward-present condition roughly resemble the waveforms of the reward-absent condition. Presumably, a stronger focus on task-relevant colors due to higher monetary incentive abolished the reward-effects seen for the low-reward condition.

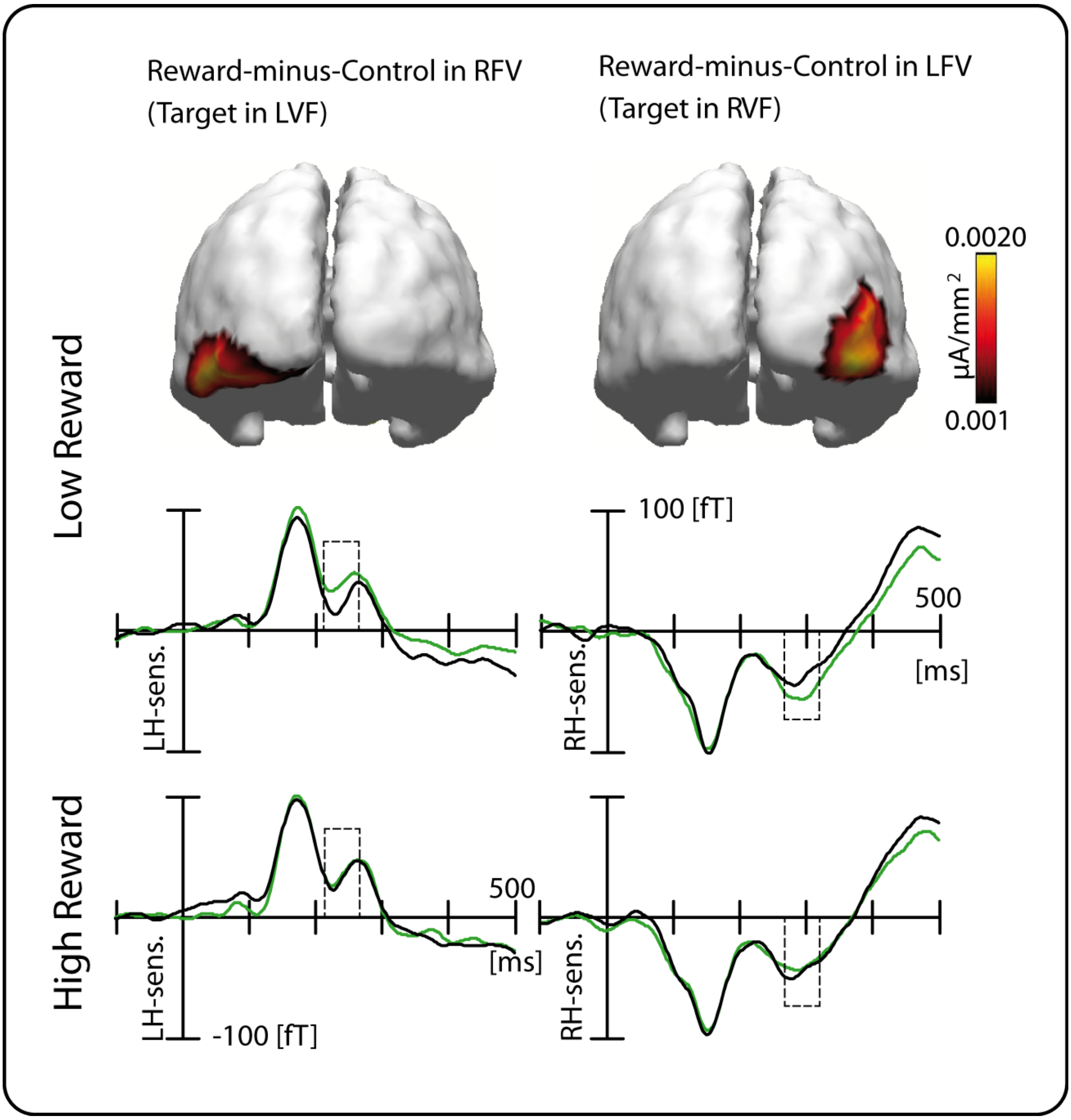

Figure 22: MEG response to search frames of Experiment 2. ERMF waveforms were elicited by non-rewarded search frames, with the reward-color being present (green waveforms) or absent (black waveforms) measured contralateral to the VF of distractor presentation. High-reward (bottom waveforms) and low-reward condition are shown separately. Respective sensors of the left and right visual hemifield are marked with RH/LH-sensor. At the top of the picture the topographical maps display the corresponding CSD distributions estimated for the reward-minus-control difference of the low-reward condition with maxima over the contralateral extrastriate cortex.

4.3 Effects to Color Probes outside the Visual Cortex for Experiment 1 and Experiment 2

Besides the fact that the high-reward condition of Experiment 2 revealed an abolished response to reward-associated color features during the search task, another finding concerning color probes distinguished this condition from the low-reward condition and Experiment 1. Here, an increased ERMF response to reward- and target-probes was found over fronto-central sensors, i.e. at sensor sites outside visual cortex areas. Figure 23 shows respective waveforms for all three probe conditions (a) and the corresponding field configuration (b) with the efflux in red over left lateral-frontal regions and the influx marked with the arrow in blue over central-parietal regions. The waveforms shown in Figure 23 illustrate that no such effect could be seen in Experiment 1 (d) and the low-reward condition of Experiment 2 (c), in which the reward magnitude was the same. In Figure 23 a the increased response elicited by reward-probes under high-reward conditions of Experiment 2 is visible with a maximum at ~170 ms after probe-onset (red arrow). Notably, this occurs roughly 20 ms prior to the earliest modulation elicited by target-probes, and 40 ms prior to the attenuation effect to reward-probes in ventral extrastriate cortex (cf. Figure 20). As marked by colored horizontal bars on the x-axis of Figure 23 a the response to reward-probes was clearly increased compared to control-probes starting approximately around 160 ms (light blue colored area), whereas the enhancement for target-probes arose later between ~200 and 270 ms with the maximum at 230 ms (light red colored area). For responses to probes under low-reward condition (Figure 23 c) no such enhancement was present, neither for reward nor for target-probes.

A rANOVA with the factors probe-condition (target, reward, control) and reward-size (low, high) was computed on the mean ERMF response between 160-180 ms. The probe-condition x reward-size interaction ($F(2,30)=3.52$, $p<0.05$) was significant and validates the observation that the enhanced response to reward-probes was only evident under high-reward conditions. For reward-size ($p=0.34$) and probe-condition ($p=0.11$) no significant main effects were observed.

The observation that the response enhancement to target-probes is only visible under high-reward condition was confirmed in the later time range between 200-270 ms with a significant probe-condition x reward-size interaction (F(2,30)=5.0, p<0.05). The corresponding main effects of probe condition (p=0.28) and reward-size (p=0.37) were not significant.

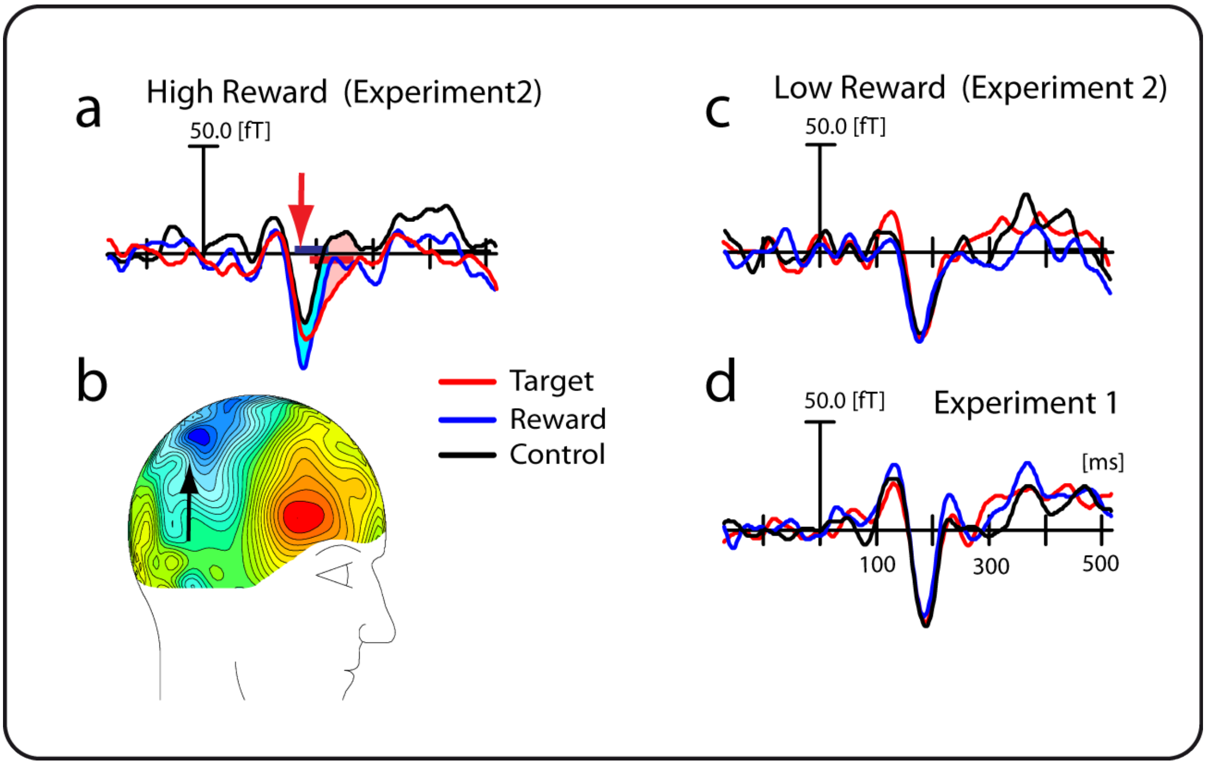

*Figure 23: MEG effects outside the visual cortex for Experiment 1 and 2. ERMF-responses to the three different probe types of the low-reward condition of Experiment 2 (**c**), of Experiment 1 (**d**), and the high-reward condition of Experiment 2 (**a**). Waveforms elicited by target-probes are drawn in red, the ones elicited by reward-probes in blue, and the ones elicited by color probes in black (Figures a, c, d). The topomap in (**b**) shows the waveform distribution for the reward-minus-control difference under the high-reward condition of Experiment 2 (light blue colored area in (a)). The black arrow marks the sensor site over parietal cortex, from where the waveforms were recorded. Here the deep blue color in the red-to-blue color scale marks an influx maximum. The small colored horizontal bars attached to the x-axis in (a) index the time range of significant amplitude differences between reward and control-probe condition (blue) and between target and control-probe condition (red). The results of a CSD analysis for the reward effect are shown in Figure 24 and the red arrow in (a) marks the respective time point.*

A sliding window t tests (see Methods section, 3.2.4 Data analysis) on the reward-minus-control and the target-minus-control differences revealed a response onset for reward-probes at 155 ms, 45 ms prior to target-probes with an onset at 190 ms. Hence, the relative time course of frontal activations relative to the modulation seen in extrastriate cortex would be consistent with the fronto-parietal activations exerting a causal influence on the modulations in visual cortex (see correlation analysis below for further supporting evidence). (see Figure 23 a)

The results of the source localization analysis (sLORETA estimates, see Methods section, 3.2.4 Data analysis) are shown in Figure 24. The reward-minus-control ERMF difference at 170 ms was overlaid onto transsections of the MNI-brain. The analysis yielded a source density maximum located at a medial frontal cortex area of the dorsal anterior cingulate cortex (dACC).

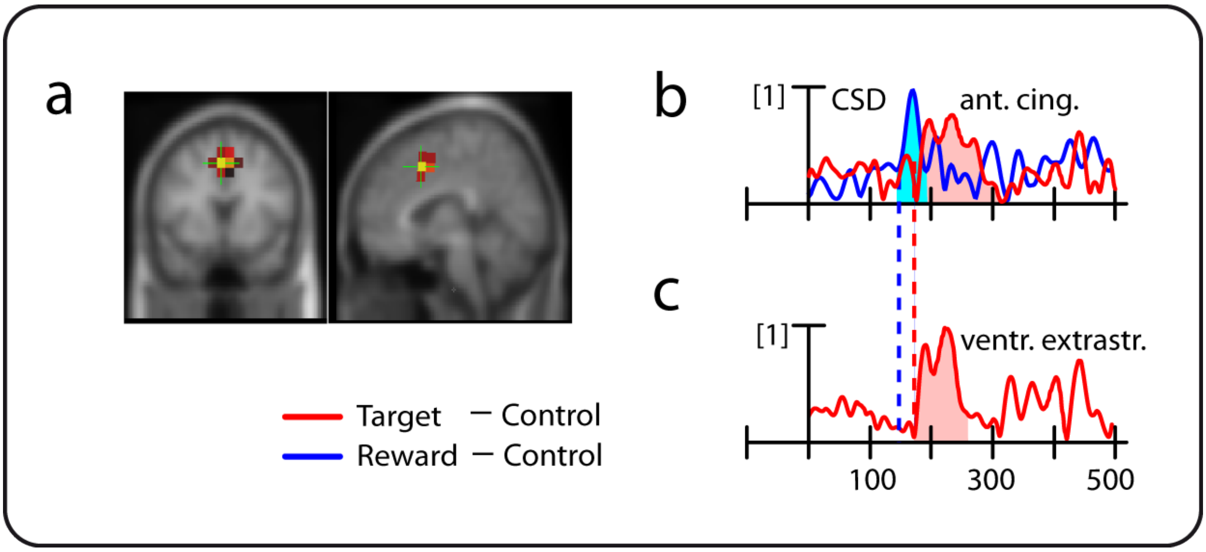

*Figure 24: Source analysis for MEG effects outside the visual cortex. For the reward effect depicted in Figure 23 a the current source density estimates (LORETA) are shown in (**a**). The difference of the reward- minus the control-condition was computed at 170 ms post stimulus, which is highlighted in Figure 23 a with the red arrow. In (**b**) and (**c**) normalized source waveforms measured from the source density maximum computations are shown. Blue traces reflect the reward-minus-control and red traces the target-minus-control ERMF difference. The normalized source waveforms in (b) are taken from the CSD analysis shown in (a) and reflect neural activity in anterior cingulate. The waveform shown in (c) was taken from the location of the ventral extrastriate CSD maximum of the target-minus-control difference of the high reward condition (green circle in Figure 20).*

For the CSD-maximum visualized in (Figure 23 a) respective source-waveforms are shown in (b). The blue trace is a difference waveform of reward- minus control-condition, while the red trace reflects the target-minus-control difference. The response to reward-probes appeared earlier than the one to target-probes. Furthermore, in line with the ERMF waveform effects shown in Figure 23 the difference waveforms in Figure 24 (b) and (c) show that the response to reward-probes in dACC (a and b) arised about 20 ms prior to the activity enhancement elicited by target-probes in ventral extrastriate cortex (c). This difference in latency is reflected by the distance between the blue and red dashed lines. In contrast, the response enhancement to target-probes in anterior cingulate reflected by the red trace in (b) did not arise prior to the response in ventral extrastriate cortex (c).

Given that the response in dACC to reward-probes under high-reward conditions of Experiment 2 appeared before the attenuation of the ERMF response in ventral extrastriate visual cortex, it is reasonable to ask whether the attenuation is linked to activity changes in dACC. Such a direct modulatory influence of frontal lobe activity on processes of attentional selection in visual cortex has been has been repeatedly documented (see section 1.5 Task and Attention Control). To address this possibility, the extent of response attenuation to reward-probes in extrastriate cortex was analyzed as a function of the amplitude and latency variation in dACC across subjects. To this end, the correlation between peak amplitude/peak latency measures in dACC (reward-minus-control ERMF difference) and the mean response attenuation between 220 and 250 ms in ventral extrastriate cortex was analyzed. This analysis revealed no correlation between amplitude measures ($r=0.213$, $t(16)=0.816$). However, a significant correlation between response latency in dACC and the amplitude reduction in ventral extrastriate cortex ($r=0.426$, $t(16)=1.76$, $p<0.05$) was found. The scatterplot in Figure 25 illustrates this correlation between response latency in the dACC and response attenuation in extrastriate cortex. It shows that subjects with progressively shorter dACC latencies showed an increasing effect of attenuation of the ERMF response to reward-probes in extrastriate visual cortex.

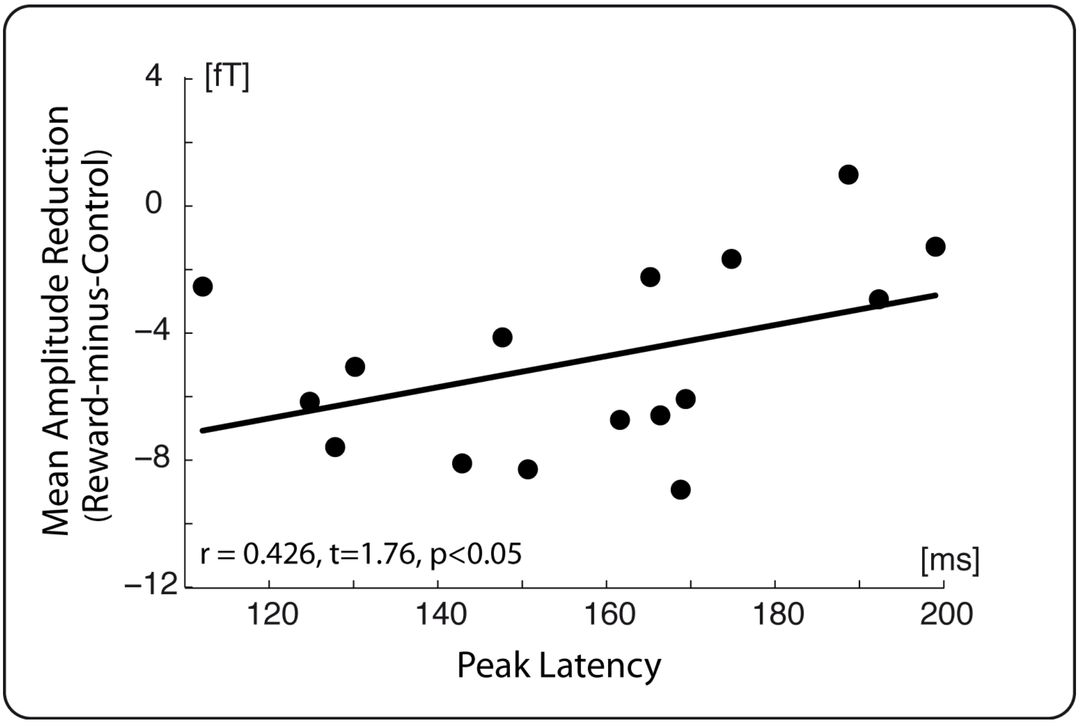

Figure 25: Correlation between effects in dACC and extrastriate cortex for the high-reward condition of Experiment 2. In the scatter diagram the mean amplitude reduction between 220-250 ms in ventral extrastriate cortex is plotted at the y-axis against the peak-response latency in dACC at the x-axis. The black dots represent every subject (n=16). The line represents the linear regression between measures.

4.4 Short Summary for the Results of Experiment 1 and Experiment 2

The attentional capture part of Experiment 1 revealed, that target-probes elicited significantly enhanced activity in extrastriate visual cortex, while the response to reward-probes was almost indistinguishable from control-probes, suggesting that a reward-relevant feature, which has no explicit task relevance, does not automatically entail modulatory effects in visual cortex. Experiment 2 confirmed this finding. After doubling the amount of money to be gained on rewarded trials, reward-probes did still not elicit an increased response in ventral extrastriate cortex as seen for the target-probes. Instead, in the high-reward condition a delayed attenuation of the response to reward-probes was observed in a more posterior ventral extrastriate region. In addition, reward and target-probes elicited an increased response in medial-frontal regions (dACC) under high-reward condition, with the response to reward-probes arising before the response to target-probes as well as before the attenuation effect in ventral extrastriate cortex. A correlation analysis revealed that the amount of delayed attenuation to reward-probes in posterior extrastriate visual cortex increased with shorter latencies of the response in ACC, suggesting a functional link between the speed of reward-representation in frontal cortex and the subsequent attenuation of sensory processing in visual areas. Finally, this observation dovetails with the differential effect of reward size on the response elicited by search arrays (spheres) in Experiment 2. The presentation of a reward-color in a non-target distractor sphere led to a response enhancement under low-reward condition. Doubling the amount of reward, however, eliminated this enhancement effect.

4.5 Experiment 3

In contrast to the irrelevant color probes in Experiments 1 and 2, the response to the search frames (spheres) showed a selection bias for the reward color in extrastriate visual cortex. Unfortunately, because of the search paradigm, the reward effect could not be compared to the effect the target color would have elicited when presented in the distractor. Experiment 3 aims at a direct comparison between the color features associated with the target and reward outside the focus of attention when subjects performed a discrimination task. To this end, the previously used search paradigm was changed such that the focus of attention was fixed in the left visual field, and the distractor sphere always appeared in the right visual field. This manipulation allowed for presenting the target color also in the distractor. The experimental design yielded four possible color assignments to the distractor: target color only (T), reward color only a (R), target and reward combined (T&R), and control colors only (C).

4.5.1 Behavioral Performance (Experiment 3)

Figure 26 summarizes the response time (a) and response accuracy data (b). The latter was generally high and comparable across the four conditions. Shown are data for the non-rewarded trials only. For accuracy this similarity of conditions was confirmed with a non-significant rANOVA with the in the four-level factor distractor condition (Control, Target, Reward, and Target & Reward) ($F(3,51)=0.118$). However, the distractor condition had an influence on response time (Figure 26 a). Subjects responded fastest on C-trials, intermediate on T- and R-trials, and slowest on T&R-trials. A respective rANOVA and post-hoc pairwise comparisons confirmed this RT pattern by yielding a significant effect of distractor condition ($F(3,51)=35.013$, $p<0.0001$). Planned pairwise comparisons revealed that all distractor conditions differed from each other ($p<0.005$), except for the statistically undistinguishable T- and R-trials ($p=0.53$).

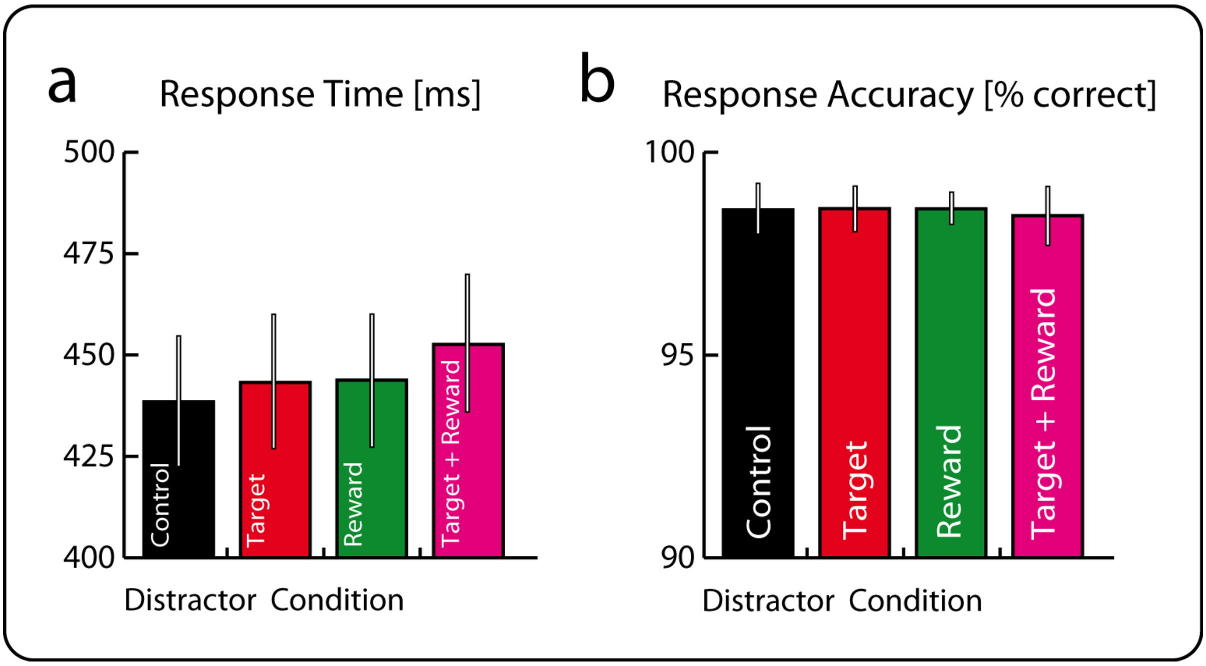

Figure 26: Behavioral performance of unrewarded trials of Experiment 3. Response time (a) and response accuracy (b) were averaged over the 18 subjects. The four conditions refer to the color assignment to the distractor spheres presented in the unattended right VF. The distractor sphere could contain two irrelevant colors in the control condition (black), the target- and a control-color in the target condition (red), the reward- and a control-color in the reward condition (green) or the target and the reward-color in combination in the target-plus-reward condition (pink). Fastest response times could be seen for the control condition, slowest for the target-plus-reward condition. The vertical white bars index the standard error of mean for every condition.

On rewarded trials, which made up 25% of all trials, the overall performance dropped by 2.2% relative to unrewarded trials. Rewarded trials only contained the three distractor conditions Target, Reward, and Control, but no Target & Reward condition. RA was 96.1% for C-, 96.7% for R-, and 96.4% for T-trials. For a comparison between rewarded and unrewarded trials a two-way rANOVA with the factors distractor condition (C, T, R) and reward (rewarded, non-rewarded) was computed. It verified the observed difference with respect to the factor reward (F(1,17)=27.7, p<0.0001). No main effect for distractor condition (F(2,34)=0.22), and no interaction between distractor condition and reward (F(2,34)=0.22) was observed. Respective RTs for rewarded C-, R-, and T-trials were 456.0 ms, 450.9 ms, and 457.5 ms, i.e. on average 13 ms slower than RTs for unrewarded trials.

The RT-effects were confirmed by a rANOVA yielding a significant main effect of reward (F(1,17)=25.1, p<0.0001). The main effect of distractor condition (F(2,34)=3.38, p<0.05) and the distractor condition x reward interaction (F(2,34)=6.95, p<0.005) were also significant.

4.5.2 MEG Responses to Unattended Spheres (Experiment 3)

Figure 27 a shows the ERMF response to the distractor spheres presented in the right visual field separately for the four possible distractor color conditions: Target (red trace), Reward (green trace), Control (black trace) and Target & Reward (pink trace). Note that waveform colors do not represent the color-coding of the Experiment. Magnetic responses at sensors contralateral to stimulus presentation at the maxima of corresponding efflux and influx field components were collapsed in the presented waveforms. To collapse responses the influx response was polarity inversed and than averaged with the efflux response. In the time range from 170-280 ms post stimulus the response to target- and reward-associated colors in the spheres was similar and both elicited significantly higher amplitudes than control-colored spheres. Remarkably, the T&R condition represented by the pink waveform elicited bigger response than T-, and R-trials. The horizontal bars, shown at the x-axis, highlight the time-range of significant (sliding window t-test, p<0.05) amplitude increases for T-, R- and T&R- trials relative to C-trials.

Notably, the enhancement of T&R-trial differences, however, turned out to be almost exactly the sum of response enhancements of T- and R-trials relative to control. This is clearly highlighted in the respective bar graph on the right (Figure 27 b) displaying the mean amplitude increase between 170 and 250 ms. Shown are the response differences Target-minus-Control (red), Reward-minus-Control (green) and Target&Reward-minus-Control (pink). The differential response for T&R is about twice as big as the response differences for target- and reward-associated colors and almost matches the algebraic sum for T-, and R-trial differences ((T-C)+(R-C)), which is displayed with the dashed grey bar on the right.

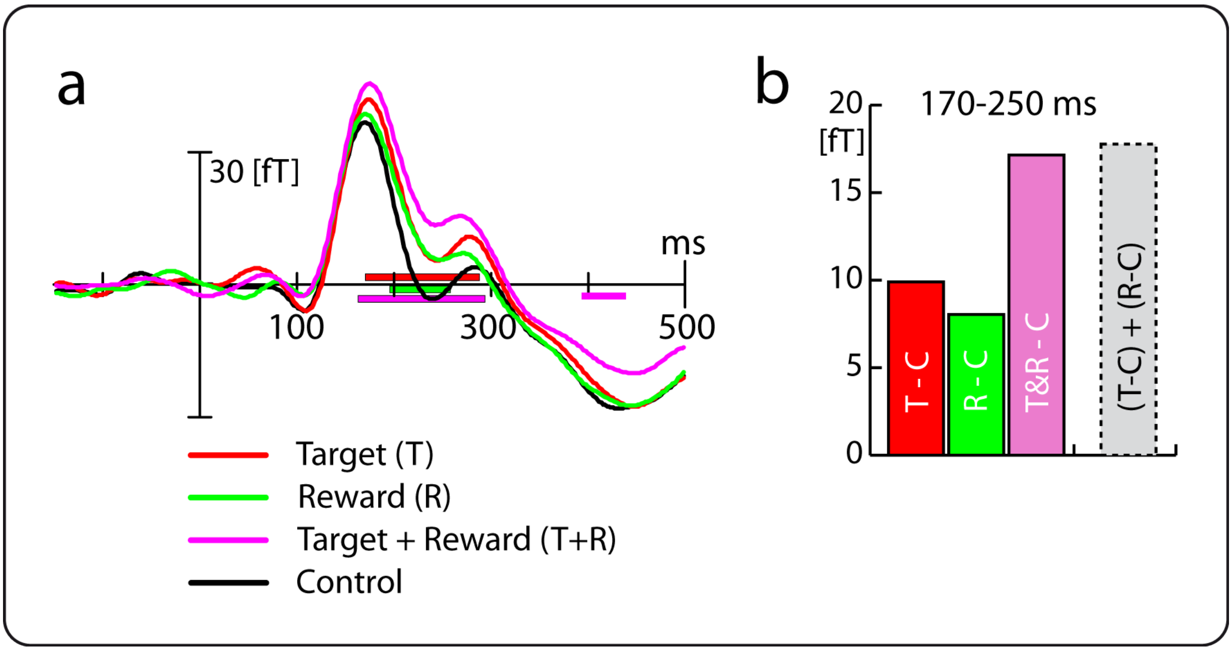

Figure 27: MEG response to distractor stimuli of Experiment 3. The waveforms on the left (a) represent collapsed responses at the field maxima over left occipital cortex marked with white and black dots in Figure 28. Responses were elicited by distractor stimuli in the unattended RVF for the Target (red), Reward (green), Target & Reward (pink) and Control (black) condition. The horizontal bars attached to the x-axis highlight the time-range of statistically significant amplitude increases of T-, R, and T&R-trials in respective colors relative to C-trials. The bar chart on the right (b) illustrates the mean response difference in a time window from 170-250 ms. The difference Target&Reward - Control (pink) is almost exactly as big as the sum of the Target - Control (red), and Reward - Control (green) amplitude, which is shown by the dashed grey column.

In Figure 28 each row shows the magnetic field distributions and 3-D source localization maps for the differences T-, R-, and T&R-minus-C are shown at 220 ms after stimulus onset. The magnetic field distributions in the middle column depict efflux with white field lines and a black dot at the maximum and influx with black field lines and a white dot at the maximum. The influx/efflux maxima over left occipito-temporal areas are very similar for all three conditions suggesting a similar cortical origin of the underlying modulations. To further investigate, if the modulatory effects due to reward and attention do really arise from the same populations of neurons in extrastriate cortex CSD distributions were estimated on the basis of the field distributions. The CSD estimates on the right are plotted above an arbitrary threshold to highlight the absolute maxima of the distribution.

Indeed, the CSD maxima for the T-C, R-C, and T&R-C differences can be seen at the same location over left ventral-lateral extrastriate cortex.

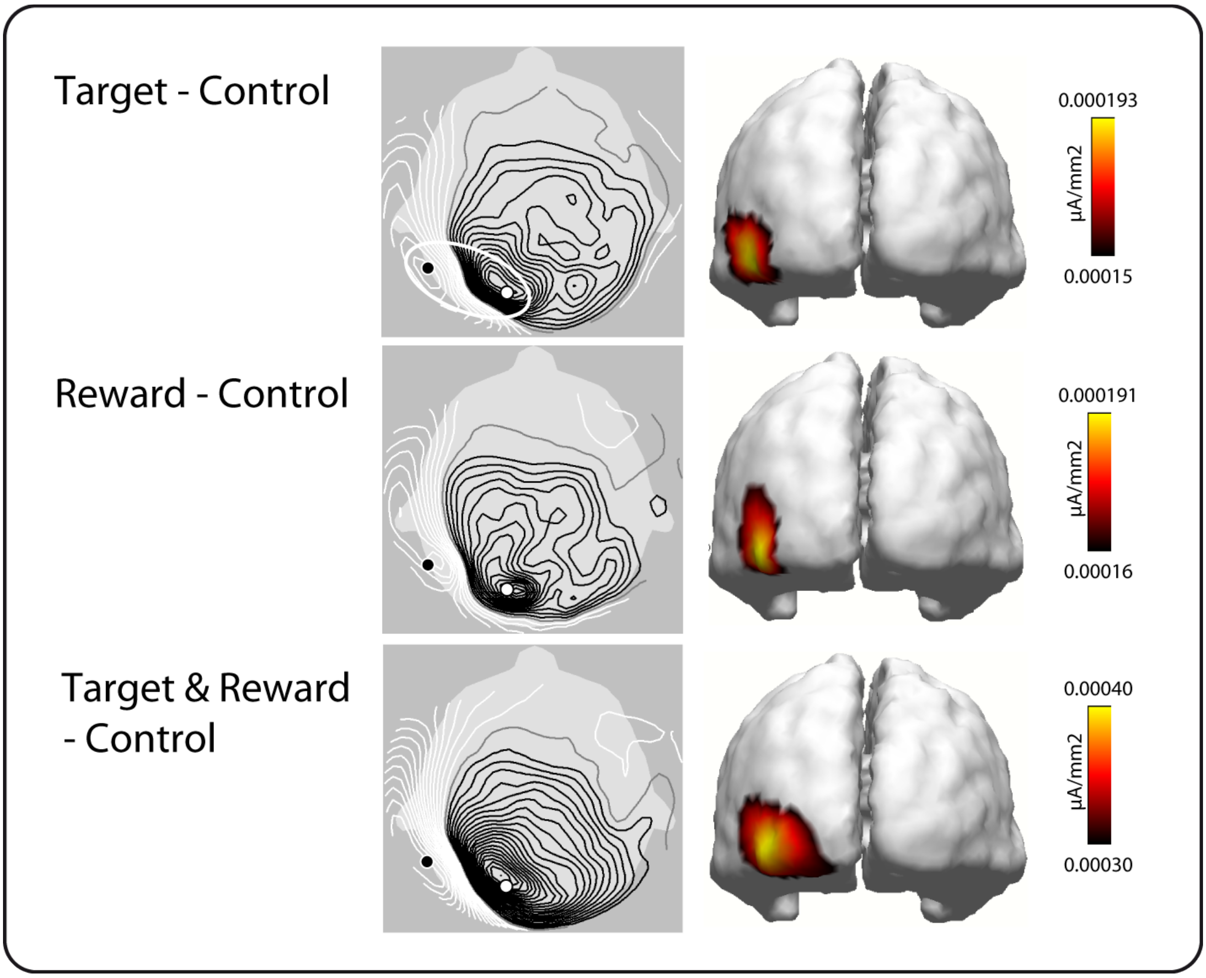

Figure 28: Magnetic field maps and CSD distributions for responses to distractors of Experiment 3. In the top-view field distributions on the left the field maxima of the influx-efflux configurations are marked with black and white dots from where the waveforms in Figure 27 (a) were recorded. All maps were computed from response differences of T-, R-, and T&R-trials minus C-trials at 220 ms after stimulus onset. The white ellipse in the left upper topomap marks the influx-efflux configuration representing the template-matching effect (as described in the following section). The CSD maps on the right show the localization of effects shown in Figure 27 and are scaled differently to highlight the current source maximum.

In sum, the observed modulatory effects due to reward and attention under task-relevant condition are additive and arise from the same area in ventral extrastriate cortex.

Notably, the response enhancement for T-trials between 170 and 280 ms as well as the localization of the effect perfectly matches the response pattern found to index global color-based attention in Bartsch et al. (2014). In this study a comparable experimental setup revealed that global color-based attention is mediated by a sequence of two functionally and anatomically separable modulations in ventral extrastriate cortex (see also section 1.3.2, Feature-based Selection). The initial phase around 200 ms, referred to as template matching phase, is thought to reflect the (mere) registration of a task-relevant feature. The later phase around 280 ms, dubbed discrimination matching phase, was indexed by a modulation in more posterior areas of the ventral extrastriate cortex, which appeared as a result of the actual discrimination of the color target. The response enhancement found for T-trials likely reflects the template-matching phase of global color-based attention. What is notable is that a similar early response enhancement is seen for the reward color in the distractor (Figure 27 & 28). The sliding-window t-test revealed that the response enhancement for R-trials arose around 200 ms which is about 30 ms later than the enhancement for T-trials (red bar), and stops at about 285 ms, i.e. 30 ms earlier than in T-trials. The duration of the effect seen for the T&R condition (pink bar) is comparable with the one seen for T condition. Beyond 260 ms the increased response to R-trials (green trace) disappears and decreases to match the one for C-trials (black trace) at about 290 ms. In this later time range, however, the enhanced response to T- and T&R-trials is still present. Hence, the later discrimination-matching phase is only present in T- and T&R-trials, but not in R-trials. This pattern of results is apparently consistent with the reward-color eliciting a template-matching effect, but no discrimination-matching effect.

The late selection process can be seen in the magnetic field distribution shown in Figure 29 b. The white ellipses highlight the respective influx-efflux configuration for the T-C and (T+R)-C differences. Hence, for the R-C difference shown in the middle topomap no late discrimination matching effect is seen. Instead, the fading field distribution of the early selection effect shown in Figure 28 is visible at a more anterior site contralateral to stimulus presentation. Figure 29 (a) shows the mean amplitude differences for T-C, R-C, and T&R-C in selected time windows from 180 ms to 300 ms after stimulus onset.

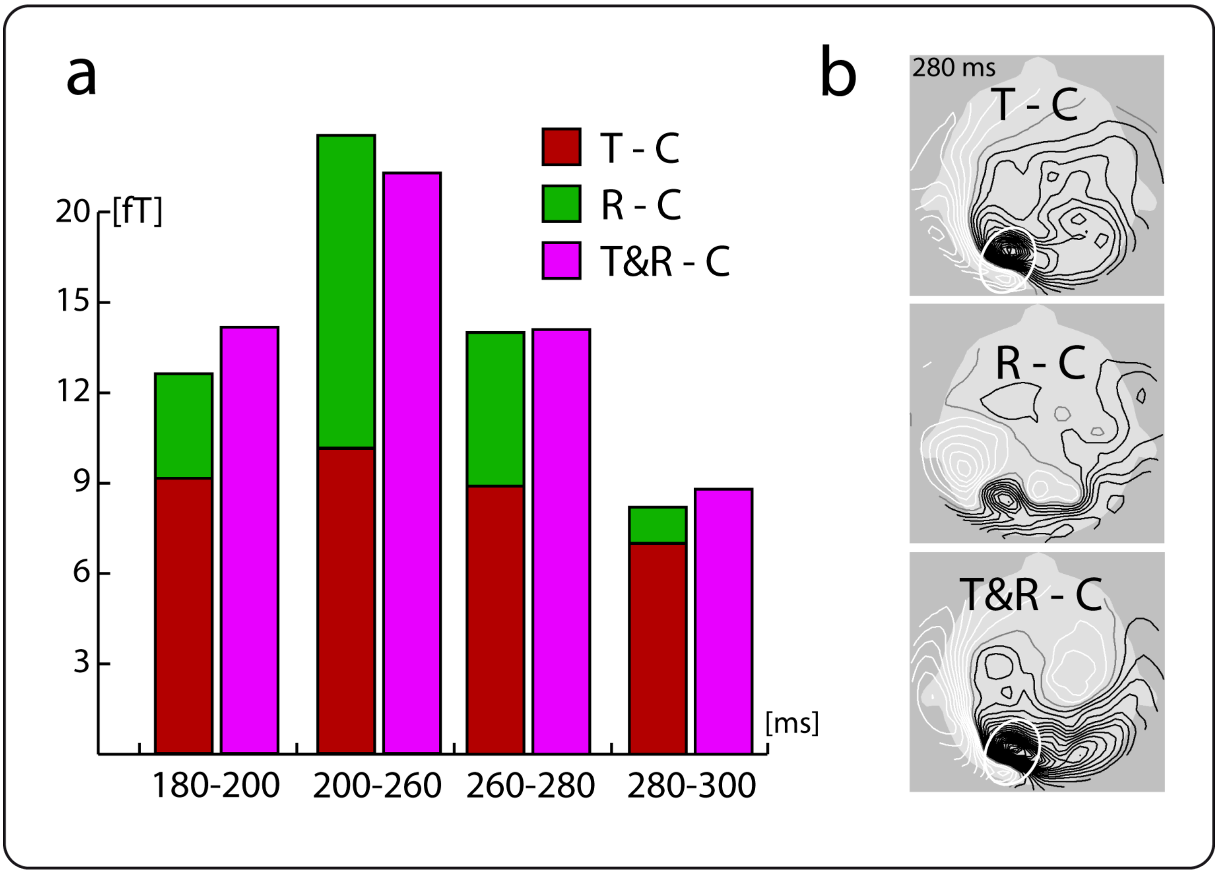

Figure 29: Mean response differences over time from 180 – 300 ms and late magnetic field distributions at 280 ms for Experiment 3. The response differences (a) facilitate a direct comparison between the amplitude sizes of the averages for T&R-C in pink, and T-C in red with R-C in green stacked atop for the four consecutive time windows. The R-C difference increases to about the same size as the T-C difference before fading towards 300 ms. The T&R-C condition almost perfectly matches the sum of T-C and R-C. In the magnetic field distributions (b) of T-C, and T&R-C the efflux-influx configurations representing the discrimination matching effect for global color selection are encircled by white ellipses, while no such effect for R-C can be seen.

Most notable, the effect size on T&R-trials matches the sum of the response enhancements to T-, and R-trials over time, even though the relative proportion of the T-C and R-C response enhancements varies. The reward effect starts to contribute to the combined target-plus-reward effect at 280-300 ms, reaches its full size at 200-260 ms at about the same magnitude as the target effect decreases towards 300 ms.

4.5.3 Short Summary for the Results of Experiment 3

Experiment 1 and 2 already showed an increased neuromagnetic response between 200 and 260 ms for distractors in the reward-color presented during visual search. With the experimental modification made in Experiment 3 a direct comparison between the distractor-color conditions (reward-, target-, and both target&reward-color) was possible. The results showed that both, the reward-, and the target-color led to similar increments in the MEG response between ~200-260 ms originating from the same extrastriate visual cortex areas. Most notable, the response to the target- and reward-color alone added up to match the response size of their combined presentation over the whole modulation time-range from ~180-280 ms.

The observed response pattern also matches the characteristics of the global feature-based attention phenomenon (cf. Bartsch et al., 2014). The reward- and the target-color elicited a comparable response around 200 ms (template matching). The subsequent discrimination-matching phase at around 280 ms was observed for the target-color, and the combined Target&Reward condition, but not for the reward-color. Taken together, the task-irrelevant reward-color elicited no discrimination-matching effect, but the initial template-matching effect, which suggests that reward became part of the task-set.

5 Discussion

The first two Experiments revealed that task-irrelevant color probes drawn in a target defining color led to enhanced neural activity between 180 and 280 ms in ventral extrastriate cortex contralateral to probe presentation. Probes matching the reward-relevant color, in contrast, elicited no such response enhancement. Not even after increasing reward-relevance by doubling the amount of money to be gained in rewarded trials (Experiment 2) did reward-probes show an enhancement relative to control-probes.

Nonetheless, reward showed an effect on extrastriate stimulus processing, when analyzing the brain response to the search frames. In Experiment 1, in the low-reward condition of Experiment 2, and in Experiment 3 the reward-color was associated with an activity enhancement contralateral to the distractor starting around 200 ms in ventral extrastriate cortex. Under such task-relevant conditions both target- and reward-associations affected the behavioral performance and the visual processing of distractor colors/objects. Notably, the ERMF response enhancement for target- and reward-color in Experiment 3 was additive and equaled the response enhancement seen for the Target-plus-Reward condition. The reward-color elicited a response comparable with the one to the target-color around 200 ms (template matching), although it was not relevant for discriminating the target. Consistently the reward-color elicited a template-matching effect but no subsequent discrimination-matching effect.

Beyond the activity modulations in visual cortex, under high-reward conditions, the color target- and reward-probes elicited response enhancements in frontal cortex structures (dACC). Here, the response to the reward-color appeared earlier (~160-200 ms) than the one for the target-color (~200-260 ms), and the onset latency of the enhancement to the reward-color correlated with the response attenuation in extrastriate cortex between ~220 and 250 ms.

5.1 Reward Effects to Color Probes (Task-Irrelevant Condition)

The results of Experiment 1 and 2 may be taken to suggest that the mere association of a color with reward, which is otherwise not part of the target-defining feature set, does not lead to a mandatory biasing of its neuronal processing in visual cortex.

This observation seems to conflict with recent studies which report increased neural responses to stimulus-features paired with reward in early visual cortex areas (Shuler and Bear, 2006, Serences, 2008, Kiss et al., 2009, Franko et al., 2010, Hickey et al., 2010) or even earlier in primate superior colliculus (Ikeda and Hikosaka, 2003). For example Serences (2008) led human observers perform a choice-task with two color gratings associated with changing reward probabilities. FMRI revealed larger BOLD responses to reward-associated gratings in early visual cortex areas, i.e. V1-V4, depending on the reward history of a stimulus and not on subjective valuation (self-reported estimates of stimulus value). Franko et al. (2010) trained two macaque monkeys to fixate and led them passively view gratings of two different orientations with one orientation consistently paired with the subsequent delivery of reward. This kind of pavlovian conditioning led to an increase in local field potentials (LFP) in V4 for the reward-paired orientation. The study provided also evidence for reward-dependent perceptual learning as the effect lasted for a while after a reversal of stimulus-reward-pairing.

Hence, evidence for reward-dependent modulations of sensory processing can be found in literature. The mentioned studies show such biasing effects in visual cortex even when the reward-defining feature is not subject to discrimination and therefore not task-relevant. However, in contrast to the present work the occurrence of a reward-feature was consistently associated with subsequent reward delivery or valuation of reward. In other words, the reward-feature cued the delivery of reward, i.e. directed attention towards the subsequent event of reward delivery or a stimulus signaling reward. This kind of reward-association did not influence performance in a negative, distracting way. In other words, there was no explicit or implicit incentive to counteract modulatory effects eventually brought about by reward-associated features.

The experimental design used here was developed to dissociate top-down definitions of reward- and task-relevance with feature biasing being probed by a distracting flash stimulus during a task-irrelevant phase of the experiment. A consequence of the design is that the appearance of the reward-color rendered any such probe primarily a distracting event than raising reward expectations.

The behavioral results for the search task of the first two Experiments revealed, that even the combination of reward and target-color in the target sphere decreased performance, i.e. the reward-color impaired target discrimination performance not only when part of the distractor but also when presented in the target sphere. The fact that the reward-feature caused distraction suggests that this feature became part of a task set and was rendered significant. It is likely then, that subjects adopted a task set in which the reward-associated color gained some priority for identification. This could also facilitate more efficient distractor attenuation/suppression for the reward-color.

Hickey and colleagues (2010) made different observations and found in their EEG studies increased responses to reward associated task-irrelevant features even after dissociating their reward contingency from endogenous attention settings. Following the considerations above, a task-irrelevant and unattended reward-feature should have a distracting impact and no positive biasing effects. Subjects searched for a shape singleton (target) among similar colored items and one color-singleton drawn in a different color (color-distractor). Color was completely task-irrelevant and subjects were given high or low reward upon correct target discrimination on every trial. Colors could swap from trial to trial, with the color of the target becoming that of the distractor or could remain the same. That is, the distractor was presented either in a color associated with high or low reward on the previous trial. Importantly, color distractors appearing in the color associated with high reward on a previous trial elicited an enhanced contralateral P1-response compared to the low-reward condition, when the same color on the previous trial was associated with low reward. An enhanced positive deflection in the P1-component typically occurs as an effect of location selection and reflects a gain-amplification of stimuli processed in retinotopically corresponding extrastriate visual areas (Hillyard and Anllo-Vento, 1998).

In this respect the results of Hickey et al. (2010) run counter to the present observations and suggest that reward-relevance of color biased processing in extrastriate cortex irrespective of task-relevance. In the present experiments no positive biasing effect was associated with the reward-color.

On the first sight the conflicting response pattern found in this work might be startling. A closer comparison of the experimental designs, however, reveals some significant differences presumably explaining these conflicting findings. The definition of task sets, differ in temporal aspects, but also regarding feature dimensions. In Hickey et al. (2010) reward was assigned to the feature color on a by trial-by-trial basis, because the color-reward association as well as reward size varied constantly from trial to trial. The present experimental conditions allowed for more consistent control settings, i.e. the color-reward association and reward size were both fixed within trial blocks. Additionally the color distractor in the experiments of Hickey and colleagues did always pop out among the presented objects only differing in shape, while the comparable distractor spheres in the present experiment did not pop out. Maybe in the present experiments subjects could adopt a stronger and more specific top-down inhibitory scheme to counter the distracting effect of the reward-color. Concerning feature dimensions there is another difference between experimental paradigms. Subjects in Hickey et al. (2010) searched for an object shape and reward contingency was only true for a simultaneously presented color not for the target-shape unlike in the present experiments, where reward- and target-association were restricted to one feature-dimension (color). The association of target and reward to two feature dimensions might be easier to handle for guiding top-down control. In Experiment 1 and 2 the target-color is unambiguously belonging to the target and the reward-color can give additional information signaling a special worthwhile target, but it can also appear in a distractor giving no information.

Taken together there is some sense in the hypothesis that reported experimental conditions cause different modes of top–down control. It may be stated again that reward-significance per se does not translate into a sensory bias in every case that would facilitate feature-selection in extrastriate visual cortex.

5.1.1 Contingent Capture and IOR

In Experiment 1 and 2 the possible biasing effect of reward was probed by distracting flash stimuli during task-irrelevant phases of the experiment using contingent capture to explore the role of reward in early visual selection. Attentional capture is typically assumed to be an automatic, bottom-up driven of process. Folk and Remington (1992), however suggested, that even stimulus-driven, bottom-up attentional processes in the visual system might not be detached from top-down cognitive influence.

There is an ongoing debate as to the circumstances under which attention is captured contingent on high-level goals or when it is purely stimulus-driven (Theeuwes, 2010). One party postulated that attention will be captured involuntarily by salient stimuli, especially abrupt onsets, irrespective to the observer´s goals or intentions (Yantis and Jonides, 1984, 1990, Theeuwes, 1991, 1992, 1994, Hickey et al., 2006). Others (Bacon and Egeth, 1994, Folk et al., 1994, Gibson and Kelsey, 1998, Folk and Remington, 1999, Yantis and Egeth, 1999, Gibson and Amelio, 2000, Lamy et al., 2004) are proponents of the contingent involuntary orienting account by Folk et al. (1992) and emphasize that previous studies demonstrating capture by abrupt onsets used paradigms in which the target itself was an abrupt onset and therefore subjects had an attentional set for onsets so that capture was contingent on onset per se (Lien et al., 2008). Maybe subjects just looked “for any target that differed markedly from its surrounding items” (Egeth et al., 2010). The theory posits that the attention-capturing effect of an onset stimulus depends on the degree to which properties of that stimulus meet top-down defined target-descriptions. (for the recent debate in more detail see Theeuwes et al., 2010) While RT measures (used by Folk et al., 1992, 1994) are only an indirect indicator for the deployment of attention, ERPs and ERMFs provide a more direct method to investigate the brain mechanisms underlying attentional capture.

The present results show a color-selective bias of neural processing in ventral extrastriate cortex for target-probes, suggesting that the increased response to the sudden appearance of a stimulus feature rendered task-relevant by top-down settings is part of the mechanism mediating capture. This observation generally lines up with a number of previous reports.

For example, Lien et al. (2008) provided evidence for attentional capture contingent on top-down control settings with an EEG experiment using the N2pc component as a direct indicator of spatial attention shifts. Arnott and colleagues (2001) replicated findings from Folk et al. (1992) measuring event-related potentials and found contingent attentional capture. In the color domain attentional capture was contingent on an attentional set and elicited an enhanced occipital N1 response contralateral to the capturing probe stimulus. Hopf et al. (2004) provided evidence for the notion that target features enhance neural activity at non-target locations.

They found retinotopically consistent enhancement of neural activity for an orientation feature in ventral extrastriate cortex prior to spatial focusing onto the target with the same orientation. Although target-probes elicited an enhanced response in extrastriate cortex most likely reflecting attentional capture contingent on top-down task settings it should be noted, that this was not reflected in performance changes. The overall IOR effect did not significantly vary as a function of probe condition. Even though target-probes produced increased extrastriate activations they were not associated with an IOR effect that differed from control and reward condition. At a first glance, this observation seems to conflict with the notion that the stronger extrastriate modulation of target-probes relates to attentional capture. However, there is data suggesting that the IOR effect might be related to neural mechanisms that do not directly depend on the extrastriate bias for target-color observed here. That is, findings of IOR have been reported for the spatial attributes of a stimulus and for objects, but for the color-domain research has typically failed to demonstrate IOR (Kwak and Egeth, 1992, Gibson and Egeth, 1994, Schreij et al., 2010). Although Law, Pratt, & Abrams (1995) could demonstrate some effects compatible with a color-based IOR, these were limited to the a special paradigm they used. The authors hypothesized, that attention (not spatially) had to be removed completely from the first stimulus and introduced a non-target distractor color between the color-cue and the color-target, which were all presented in the same central attended location. This is a situation, which is not comparable with the present experimental conditions. Taking into consideration that the probes were flashed unpredictable in time and occurred in one of two possible unattended locations, the mere onset of the probes may have caused IOR as a consequence of spatial orienting.

So the observed color-selective bias might not influence the IOR effect any further. To this regard Busse et al. (2006) had interesting findings for an experiment with two superimposed moving random dot arrays in both VFs. Effects of exogenous cuing were investigated for different cue-target combinations. A change in motion direction served as target, and the preceding cue could either be a color change or also a change in motion direction in one of the two superimposed dot arrays, yielding in spatial (valid/invalid) and featural (same motion direction or not) components.

For long cue-target SOAs (600-800 ms) valid versus invalid cues produced the typical IOR effect, whereas the validity of motion-direction cues did not give rise to any IOR. The only effect found for the motion feature, was one of facilitation in an early time-range for targets with both, valid location and valid motion direction. For the present experiments there is also the possibility of a facilitation effect for target-probes causing a stronger location-bias with the consequence of facilitated performance in target-selection after valid target-probes. However, such facilitating effect would be expected to appear for SOAs much shorter than the ones used in the present experiments (600-900 ms) (Hopfinger and Mangun, 1998). Taken together it is most likely, that the observed IOR effect here is based on the sudden onset of probes, but excluding the color-domain of features.

5.2 Reward Effects to Distractor Spheres (Task-Relevant Condition)

5.2.1 Global Color-Based Attention

The reported neuromagnetic responses to unrewarded trials revealed increased responses to target (onset at 170 ms) and reward associated color (onset at 200 ms) compared to control. The target-, but not the reward-color showed a later second phase modulation around 280 ms over more posterior visual cortex. This neural signature for the target-color replicates findings of global feature-based attention observed for color (Bartsch et al., 2014). A similar effect has also been found for the orientation feature (Bondarenko et al., 2012). Global color-based selection was characterized having two steps, firstly the initial template matching phase around 200 ms reflecting the mere presence of a target-defining color, secondly the discrimination matching phase around 280 ms reflecting color selection in the unattended distractor as a result of the discrimination process in the focus of attention. Notably, the initial phase seems to reflect a preset selection bias for any color being part of an attentional task set for task-relevant features, because it was also found for a task-relevant distractor color not present in the target. The exciting finding in this work was, that such template-matching effect was also found for the reward-color, which was not target-defining, but obviously part of the color template due to its behavioral relevancy, even though being irrelevant for the execution of the task. In a recent fMRI study Serences and Saproo (2010) also provided evidence for reward-dependent global feature selection outside the focus of attention. Subjects performed a forced-choice task on two orientation stimuli (gratings) in left and right VF, while simultaneously learning to associate reward sizes (high/low) to specific orientations. They analyzed BOLD responses (orientation-selective voxel tuning functions) in respect to orientation of the grating, the associated reward magnitude and whether the grating was attended or not. An orientation associated with high reward elicited a stronger and more tightly tuned response in early visual cortex areas than low-rewarded gratings. And this was found to be independent of the focus of attention as the effect was found for voxels retinotopically corresponding with the attended as well as the unattended stimulus grating.

The results of this study support the present findings of reward modulating feature selectivity in a spatially global way outside the focus of attention.

Even though target and reward associated colors both elicited a template matching effect with a strong similarity in size and cortical origin, there were two major differences regarding onset of the template matching effect and the subsequent discrimination matching effect. The template-matching effect for Reward appeared at ~200 ms with a delay of ~30 ms relative to Target suggesting a temporal priority of the target-color over the selection of the reward-color. The present paradigm aimed at the separation of top-down definitions of target and reward, so that reward rendered rather distracting than helping task performance, with the latter being reduced for rewarded relative to unrewarded trials. This observation is consistent with the relative temporal priority of the template matching effect for the target feature under present experimental conditions. This is by no means absolute. With a different experimental setup, for example when target- and reward-associations for features overlap, reward has been found to facilitate attentional selection eliciting an earlier N2pc component (Kiss et al., 2009). The missing discrimination matching effect for the reward-color could also be ascribed to the paradigmatic separation of reward and target features. Bartsch et al. (2014) found this later effect around 280 ms only for distractor colors also present in the target and only when the target object containing the color was under discrimination. In the present experiment this was impossible, as the reward-color was always without task-relevance and therefore not under discrimination and not part of the target object, because only non-rewarded trials were analyzed. Therefore the missing discrimination effect was expected. Notably, it is possible that the late discrimination effect of global color-based attention is not only color-based, but relies on a form of object-based selection (e.g. Schoenfeld et al., 2014) as well. The target-color in the distractor sphere and in the target sphere do not form an object in perception, but they are linked in their task-relevance.

Another interesting finding for Experiment 3 were the additive template-matching effects of reward and attention (Figure 29).

That is, the Target&Reward condition for the combined presence of target- and reward-color in one sphere elicited the same enhanced response in ventral lateral extrastriate cortex as the sum of both enhancements to reward-, and target-color presented separately throughout the complete modulation time-range (180 – 300 ms). Again, it is the separate definition of target- and reward-relevance, which might have forced subjects to form separate templates for both feature categories. Even if reward elicits global feature based selection, it might be special in terms of top-down control. However, based on the present data the possibility that subjects built a compound template for reward and target together - as presented in the sphere - cannot be excluded. The T&R response enhancement would be 100% and the individual T- and R-trials would have a partial match with round about 50% response enhancement each or in respective proportions yielding 100% together. The fact, that the template-matching effect for reward occurred with an onset latency, speaks against a compound template. For a compound template one would expect a common onset for the modulations of its components. On top of that, there is growing literature, describing reward as a more durable variable in terms of top-down control than a common attentional set. Anderson et al. (2012) found that stimulus-reward associations learned in one task can generalize on another task, and that stimuli signaling reward-delivery in one task, but serving as distractor in another task, involuntarily capture attention over half a year later (Anderson and Yantis, 2013). A persistent effect for reward-feature-selection is also true for stimulus-reward associations changing within the task (Hickey et al., 2010) or when the reward-association is not in effect any more (Della Libera and Chelazzi, 2009). That reward effects persist despite and beyond changing attentional settings, make two separate templates more likely than a composed template for reward and attention.

5.2.2 Inhibitory Effects due to Reward

The search task of all three experiments involved two spheres of which one contained the target and the other one served as distractor. The presence of the reward-color (in Experiment 3 also the target-color), in the distractor resulted in decreased task performance relative to control-colors. Doubling the amount of reward to be gained in under high-reward condition of Experiment 2 led to the same behavioral response pattern than under low-reward condition.

This observation is noteworthy, because it does not match the neuromagnetic response pattern. The response to the presentation of the reward-color in the distractor sphere led to a neural response enhancement under low-reward conditions in Experiment 2, which could also be observed for Experiment 1. Doubling the amount of reward, however, eliminated this enhancement, suggesting effective top-down inhibitory control to eliminate reward-contingent effects (see 5.3.1 Top-Down Inhibitory Control of Reward). In terms of RA and RT the amount of decrement, however, was uninfluenced by reward size. One could predict, that increased top-down inhibitory control for reward-associated stimuli under high-reward condition should result in less behavioral distraction. As this is not the case, the unchanged response pattern might not reflect the same situation as under low-reward condition, but an already suppressed state. Without top-down control an even greater impact of reward on task performance is thinkable. But if we assume that top-down inhibitory control aims at proper task execution the response pattern under high reward conditions is likely to reflect the consequence of top-down distractor attenuation. Of course, the validity of this interpretation cannot be warranted on the basis of the present data.

5.3 Top-Down Effects for Reward

5.3.1 Top-Down Inhibitory Control for Responses to Color Probes

Experiment 1 and 2 revealed that task-irrelevant probes drawn in the target-color led to increased neural responses (180-280 ms) in contralateral ventral extrastriate cortex. In contrast, color probes associated with reward showed no such response enhancement. Instead, under high-reward condition in Experiment 2 reward-probes produced a delayed response reduction (~220-250 ms) relative to control-probes. Together with the effects for the distractor spheres reported in the previous section these observations suggest that reward contingent modulatory effects in extrastriate visual cortex are either not present for capture stimuli or under effective inhibitory top–down control. Specifically, reward-related biases of sensory stimulus processing in extrastriate visual cortex could have been present. But they may have been effectively eliminated or even suppressed by top–down inhibition. In Experiment 2 such top–down inhibition was indeed seen with increased reward-relevance.

In section 1.4 “Contingent Attentional Capture” the “signal suppression hypothesis of controlled attention capture” by Sawaki and Luck (2010, 2011, 2013) was introduced. According to this account all salient irrelevant distractor items are detected by the visual system thereby causing an attend-to-me signal. The attend-to-me signal could be overridden by top-down suppression, which is reflected by the Pd component. The signal suppression hypothesis of Sawaki and Luck is consistent with the results for capture probes in this work. Under high-reward conditions of Experiment 2 the general attenuation of the probe-elicited response suggests that such counteracting suppression appeared to some extent for all probe types. The attenuation to high-reward probes in the later time range from ~220-250 ms peaking about 30 ms after the response to target-probes may correspond with an increased distractor positivity component. For the low-reward condition a suppression of smaller amplitude might have just cancelled a positive modulation bias as seen for target-probes.

An effect of reward on present experiments is supported by the behavioral data, because RTs were slower under low- than under high-reward conditions.

The mere presence of the reward-color led to a performance decrement in the first two experiments and in Experiment 3 reward presented in the in the non-target sphere also had a distracting effect.

In contrast to behavioral data the MEG responses for the target, but not the reward-probes showed a significant response enhancement relative to control-probes under both low- and high-reward condition. This is an observation in line with the contingent involuntary orienting account (Folk et al., 1992). According to this theory, the attention-capturing effect of an onset stimulus depends on the degree to which properties of that stimulus meet the top-down definitions for the target stimulus (see section 1.4 “Contingent Attentional Capture”). Evidence for such contingent attentional capture in visual areas was proofed with an ERP-study by Arnott et al. (2001). Using the paradigm of Folk et al. (1992) they found that attentional capture contingent on a task-relevant color (or onset stimuli) elicited an enhanced occipital N1 response contralateral to the capturing probe stimulus. That task-irrelevant distractor stimuli sharing a target feature (e.g. orientation) are associated with a retinotopically consistent enhancement of neural activity shows that visual search relies on top-down settings for a task-relevant feature (Hopf et al., 2004).

5.3.2 Effects Outside the Visual Cortex

As mentioned above reward-probes were not associated with increased responses relative to control-probes in visual cortex. However, under high reward conditions reward-probes elicited an enhanced response in dorsal anterior cingulate cortex (dACC) with a maximum at 170 ms (see Figure 23). Target-probes also elicited an enhanced response in dACC, which had a smaller amplitude and a maximum roughly 20 ms after the maximum for reward-probes. Notably, under low reward conditions a dACC-effect appeared neither for reward- nor for target-probes. Consistent with the low-reward conditions of Experiment 2, in Experiment 1 no such dACC modulation was observed.

In sum, the present experiments suggest that reward effects are under strong top-down inhibitory control. This preferrably inhibitory effect may relate to specific features if the experimental setup.

First, the reward-color had a generally distracting effect as indexed by the decrement in task performance due to the mere presence of the reward-color during visual search all three Experiments. Second, overall faster RTs under the high- than the low-reward condition of Experiment 2 match the finding that activity modulations in extrastriate cortex were generally smaller under the high- than under the low-reward condition. It is plausible to assume that subjects generally aimed at better task performance under high-reward conditions, which made them less distractible due to the response attenuation in visual sensory cortex. Furthermore, under the high-reward conditions the earliest response enhancement to reward-probes was seen in dACC. That this response enhancement appeared before the response attenuation in ventral extrastriate cortex has a strong implication for a causal relationship. Indeed, evidence in support of a causal relationship was observed, as the latency of the dACC response was found to correlate with the amount of attenuation in extrastriate cortex (Figure 25). This presumably causal relation lines up with experimental data suggesting that the dACC is involved in the top–down (inhibitory) control of extrastriate sensory processing. For example, Danielmeier et al. (2011) found error-related neural activity modulations in human posterior medial frontal cortex with fMRI that correlated with the suppressed activity in sensory visual cortex areas encoding task-distracting stimulus features. Also, the dACC is an area known to be involved in conflict-monitoring and executive control (Schall et al., 2002, Botvinick et al., 2004, Mansouri et al., 2009) and it is anatomically suited to link action and reward. ACC receives projections from orbito-frontal cortex, striatum and the mesolimbic dopamine system, which are all linked to reward processing, and DLPFC and supplementary and primary motor cortices, which are structures known to process locations and actions (summarized in Hayden and Platt, 2010). With single-cell recordings in monkeys Hayden et al. found neural activity in ACC is linked to fictive and experienced reward, and predicts saccade execution (Hayden et al., 2009, Hayden and Platt, 2010). Recently, Hickey et al. (2010) observed such a correlation between ACC activation and the reward-associated deployment of attention. They correlated reward processing in anterior cingulate cortex with behavioral performance measures (RT) and found that reward-magnitude dependent ACC activation predicted the deployment of attention.

For the present data the dACC activation could partly be explained by the conflict for the reward-relevant color being salient, but task-irrelevant and distracting. Likewise target-probes were task-relevant and distracting and also associated with a dACC activation. These results appear to align with the recent proposal that the dACC is a key part of a cortical system maintaining task-sets (Dosenbach et al., 2006). The increased magnitude of monetary reward may have caused the task- and reward-associated color probes to be more potent in capturing attention. Then, the increased neural response found in dACC may have served to neutralize the bias for probes drawn in these colors, and therefore attenuate distraction and maintain the performance focus on the task-relevant search frames. The system that maintains task-sets might operate upon cues signaling increased demands on attentional control (Weissman et al., 2004, Weissman et al., 2005). The announcement of a high-reward block could have motivated subjects to actively orient away from the salient cues (target, reward) towards the visual search part (Woldorff et al., 2004). Of course, on the basis of the present data one can only speculate about the actual processes involved.

5.4 Reward or Attention?

All present experiments showed extrastriate modulations for a color-feature associated with reward during the target selection. In Experiment 3 the response pattern to the reward-color presented in the distractor showed a perfect match in term of amplitude and localization in extrastriate cortex for the template-matching phase of global feature-based attention (cf. Bartsch et al., 2014). If the same initial process underlying global-feature based attention is also elicited by a reward-associated feature one might assume that reward-biasing is simply brought about by attentional mechanisms. Chelazzi (2013) et al. recently developed a concept of how reward can influence visual selection. Based on a survey of the literature the authors proposed that reward might “teaches” visual attention via several mechanisms leading to a facilitation of sensory selection. Depending on experimental context and requirements, rewards could either motivate stronger top-down attentional engagement (explicit biasing), or implicit event-reward pairings may bias attentional selection akin to perceptual priming. In all cases, Chelazzi and coworkers propose reward effects to be attention-mediated, with the consequence that they are indistinguishable from effects to attention. Confirming experimental evidence comes from recent observations in monkey visual cortex. Stanisor et al. (2013) found that firing effects of reward and attention in V1 perfectly overlapped and suggest common underlying selection mechanisms. Of course, MEG recordings do not allow us to decide, whether the exact same neurons contributed to the global feature-based selection effects of reward and attention.

Nonetheless, the selection effects in extrastriate cortex very likely reflect attentional modulations, but the origin of top-down control may not necessary be the same. In fact some of the present observations speak in favor of different top-down modulatory influences. Firstly the effects of Target and Reward in Experiment 3 were additive, but had different onset latencies. The relevance of reward and attention may be coded in separate areas of the prefrontal cortex, but their modulatory influence may converge on the same region in sensory cortex areas.

Orbito-frontal (Tremblay and Schultz, 1999, Schultz et al., 2000, Hikosaka and Watanabe, 2004, Padoa-Schioppa and Assad, 2006, Roesch and Olson, 2007) and dorso-medial fontal cortex, like the ACC (Gehring and Willoughby, 2002, Hayden et al., 2009) are often described to encode value. Visual selective attention is rather controlled by dorsolateral prefrontal cortex areas, in particular by the FEF (Moore et al., 2003, Moore and Fallah, 2004, Armstrong et al., 2006, Armstrong and Moore, 2007, Heitz et al., 2010), for which direct connections to extrastriate visual cortex are known. So independent top-down influences from orbito-frontal/dorso-medial and dorsolateral-prefrontal cortex may converge on feature-selective neurons of the ventral-stream extrastriate cortex, where an additive bias is measurable.

As an alternative, it is possible that value and attentional priority are represented independently in the same cortical structure. In such control structure their effects might be combined and an already added up signal would be transferred via a common top-down pathway to bias feature processing in visual cortex. Area LIP (lateral intraparietal) is a possible cortical control structure suitable to encode such biasing signal. LIP has been has been proposed to merge top-down behavioral goals and bottom-up saliency in a unified priority map that guides visual selective attention (Ipata et al., 2009, Bisley and Goldberg, 2010). Moreover, LIP has been found to code attention and reward value independently (Platt and Glimcher, 1999, Sugrue et al., 2004, Bendiksby and Platt, 2006, Peck et al., 2009, Louie et al., 2011). Hence, LIP may compute a priority signal reflecting the added effects of attention and reward, so that the single modulation for both entities, but also the combination of attention and reward would modulate visual selection in extrastriate cortex.

Taken together, whatever the top-down mechanisms are that mediate the combined effect of attention and reward, both lead to the same sensory modulation in extrastriate visual cortex suggesting that the modulatory consequence at the site of selection is largely overlapping.

Still, the results for the visual search part and the attentional capture part of this work give rise to partially conflicting interpretations. Distractor spheres containing the reward-color were associated with an enhanced response, as were distractor spheres containing the target-color. Color probes, instead, showed an enhanced response to the target-color, but no enhancement for the reward-color.

As mentioned above the reward-probes may not have been associated with an enhancement effect because a top-down inhibitory signal from frontal or parietal control-structures perfectly cancelled the effect (Experiment 1), or even produced a delayed suppression of the effect. An alternative is that no bias for the reward-probes appeared because the feature was presented at a completely task-irrelevant period of the experimental trial, where subjects were effective in eliminating the feature bias that is not performance-relevant at all. The bias for the performance-relevant target color, however, could not be eliminated, as on half of the trials the next stimulus frame could have been the next target. Hence, it is plausible to always bias the target color for optimal preparation to discriminate the target. During target discrimination, that is, when feature discrimination is required to perform the task, subjects may not be able to uphold a completely selective feature bias for only the target color, even though the top-down definition of task- and reward-relevance are operationally dissociated. The latter alternative, however, runs to some extent counter to the fact that there was a late attenuation for reward-probes under high-reward conditions in Experiment 2. In other words, the reward-feature was presumably a part of the top-down template for onset stimuli in general and independent of the sphere task.

In closing, it is clear that the results of the three reported experiments cannot decide among those alternatives. Further experiments are surely necessary for clarifying the issue.

5.5 Conclusion

The reported experiments together show that when top-down settings for task- and reward-relevance are kept non-overlapping, the mere association of an item feature, like a particular color, with reward does not lead to an automatic sensory biasing of its selection in visual cortex. The biasing effect of reward turns out to critically depend on stimulation conditions and task requirements. Reward relevance led to increased feature responses during target discrimination but not during the presentation of task-irrelevant color probes. Increasing reward relevance was indexed by a general suppression of the sensory bias of the reward-color during both task-relevant as well as task-irrelevant phases of the experiments. Finally, under high-reward conditions response enhancements were seen in dorsal anterior cingulate cortex (dACC) for both the reward- and the target-defining color. Most notably the onset of the reward-associated dACC effect appeared prior to the target-associated effect, with the onset-latency of the former (inversely) correlating with the amplitude reduction in ventral extrastriate cortex. I propose here that the dACC activation reflects the manifestation of the subjects strategic top-down control adjustments to improve performance under high-reward conditions.

Experiment 3 revealed that reward-associated modulations in visual sensory cortex closely resemble the template-matching phase of global feature-based attention reported in Bartsch et al. (2014). These findings suggest independent top-down influences for attention and reward, with the modulatory effects in visual cortex being indistinguishable, because attention is the common denominator to bias visual selection.

In sum, this work provides evidence for reward influencing early visual stimulus processing. In case reward information hinders task-performance, this influence can appear in form of sensory suppression to avoid a counterproductive reward-bias.

Further research is needed to identify the nature of top-down influences underlying reward and attention.

List of Abbreviations

Nomenclature of brain areas

ACC	anterior cingulate cortex
dACC	dorsal anterior cingulate cortex
DLPFC	dorsolateral prefrontal cortex
FEF	frontal eye fields
IT	inferior temporal
LGN	lateral geniculate nucleus
LIP	lateral intraparietal cortex
LO	lateral occipital cortex
LOC	lateral occipital complex
LPFC	lateral prefrontal cortex
MT	middle temporal area = V5
msFC	medial superior frontal cortex
PFC	prefrontal cortex
PO	parieto-occipital area
PPC	posterior parietal cortex
SC	superior colliculus
TE	anterior inferior temporal cortex
TEO	posterior inferior temporo-occipital cortex
V1	visual area 1
V2	visual area 2
V3	visual area 3
V3a	visual area 3 anterior
V3/VP	visual area 3 ventral part
V5	visual area 5 = MT
V4	visual area 4
V4v	visual area 4 ventral
V7	visual area 7
V8	visual area 8

General Abbreviations

BOLD	blood-oxygenation-level-dependent (fMRT)
CSD	current source density
CTOA	cue-target onset asynchrony
EEG	electroencephalography
EOG	electrooculogram
EPSP	excitatory postsynaptic potential
ERMF	event-related magnetic field
ERP	event-related potential
FBA	feature based attention
ICBM	International Consortium for Brain Mapping (MNI brain)
IOR	inhibition of return
IPSP	inhibitory postsynaptic potential
ISI	inter stimulus interval
fMRI	functional magnetic resonance imaging
LFP	local field potentials
LVF	left visual field
MNI	Montreal Neurological Institute (standard brain)
MNLS	minimum norm least squares
MEG	magnetoencephalography
PET	positron emission tomography
rANOVA	repeated measures analysis of variance
RA	response accuracy
RF	receptive field
RT	reaction time
RVT	right visual field
SDE	source density estimate
sLORETA	standardized low resolution brain electromagnetic tomography
SOA	stimulus-onset asynchrony
SQUID	superconducting quantum interference device (MEG)
VF	visual field

List of Figures

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