



Overt and covert attention to location-based reward

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ARTICLE INFO

Keywords:

Reward
Spatial attention
Covert attention
Overt attention
Eye movements

ABSTRACT

Recent research on the impact of location-based reward on attentional orienting has indicated that reward factors play an influential role in spatial priority maps. The current study investigated whether and how reward associations based on spatial location translate from overt eye movements to covert attention. If reward associations can be tied to locations in space, and if overt and covert attention rely on similar overlapping neuronal populations, then both overt and covert attentional measures should display similar spatial-based reward learning. Our results suggest that location- and reward-based changes in one attentional domain do not lead to similar changes in the other. Specifically, although we found similar improvements at differentially rewarded locations during overt attentional learning, this translated to the least improvement at a highly rewarded location during covert attention. We interpret this as the result of an increased motivational link between the high reward location and the trained eye movement response acquired during learning, leading to a relative slowing during covert attention when the eyes remained fixated and the saccade response was suppressed. In a second experiment participants were not required to keep fixated during the covert attention task and we no longer observed relative slowing at the high reward location. Furthermore, the second experiment revealed no covert spatial priority of rewarded locations. We conclude that the transfer of location-based reward associations is intimately linked with the reward-modulated motor response employed during learning, and alternative attentional and task contexts may interfere with learned spatial priorities.

1. Introduction

Current understanding of visual selective attention indicates that both covert and overt attention (attending to a location in our periphery or making an eye movement to that location) are linked by a common neural architecture, by means of a shared frontoparietal network (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta, 1998; de Haan, Morgan, & Rorden, 2008). The extent of this overlap has, however, been controversial. The premotor theory of attention proposed by Rizzolatti, Riggio, Dascola, and Umiltà (1987) postulated that covert attention is akin to the programming of an eye movement. Evidence in support of this theory comes from studies reporting higher detection accuracy at a target location coinciding with the endpoint of a saccade (Deubel & Schneider, 1996; Dore-Mazars, Pouget, & Beauvillain, 2004), better target detection at a saccade goal even when explicitly directed to attend somewhere else (Hoffman & Subramaniam, 1995), and a gradual build-up of attention at a saccade goal, reaching a peak immediately prior to saccade onset (Deubel, 2008; Dore-Mazars et al., 2004). Investigation of the frontal component of the oculomotor network, the frontal eye fields (FEF), has revealed disruption of saccades and shifts in spatial attention after applying transcranial magnetic stimulation (TMS) or microstimulation to FEF neurons

(Beckers, Canavan, Zangemeister, & Homberg, 1992; Moore & Fallah, 2001). Furthermore, microsaccades or 'fixational eye movements' observed during covert visual search (Martinez-Conde, Macknik, & Hubel, 2004; Martinez-Conde, Otero-Millan, & Macknik, 2013) likely reflect covert attentional shifts (Engbert & Kliegl, 2003; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008), supporting the concept of a common oculomotor neural underpinning for overt saccades and fixational eye movements in covert attentional settings.

However, there have also been numerous studies which report findings not in line with the predictions of premotor theory, including the ability to endogenously attend to stimulus locations other than the saccade goal without disturbing the eye movement (Kowler, Anderson, Doshier, & Blaser, 1995), and a lack of facilitation of visual perception for probes presented at a saccade goal (Hunt & Kingstone, 2003). In a recent review, Smith and Schenk (2012) suggest that the main consistent finding from studies on premotor theory is that only exogenous (stimulus-driven) attention is dependent on saccade preparation (Henik, Rafal, & Rhodes, 1994; Sereno, Briand, Amador, & Szapiel, 2006; Smith & Ratcliff, 2004). In their study examining the time-course of exogenous and endogenous effects, Belopolsky and Theeuwes (2012) found that although saccade preparation accompanied shifts in covert

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attention due to both exogenous and endogenous (goal-driven) cues, the saccade program to the attended location for endogenous cues was suppressed shortly after a covert attentional shift had been completed. Smith and Schenk (2012) propose that an alternative to premotor theory, the biased competition account of visual attention (Desimone, 1998; Desimone & Duncan, 1995), may provide a more appropriate framework to incorporate the empirical findings garnered from assessing the validity of premotor theory. In the biased competition account, competition between neural representations is integrated across sensory and motor systems, converging on a single ‘winning’ representation. Physically salient items in the environment have a strong representation, but competition may also be biased towards less physically salient stimuli by endogenous factors such as current goals in working memory (Soto, Hodson, Rotshtein, & Humphreys, 2008). The lateral intraparietal area (LIP) in the parietal lobe and the FEF have been implicated in target selection in both covert attention and saccades, comprising selective spatial receptive fields (Bisley & Goldberg, 2010; Thompson & Bichot, 2005). LIP in particular has been proposed to act as an integrated priority map of top-down and bottom-up signals for behaviorally relevant stimuli (Bisley & Goldberg, 2010).

Attentional orienting has generally been described in terms of exogenous and endogenous control (Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Theeuwes, 2010). In recent years, it has been suggested that these two forms of attentional orienting do not fully account for the behavior and biases observed in the attentional orienting literature (Awh, Belopolsky & Theeuwes, 2012). Much research has shown that stimuli associated with reward can capture attention and the eyes, even when attending to the rewarded stimulus contradicts selection goals (Anderson, Laurent, & Yantis, 2011a,b; Failing & Theeuwes, 2014; Hickey, Chelazzi, & Theeuwes, 2010; Le Pelley, Pearson, Griffiths, & Beesley, 2015; McCoy & Theeuwes, 2016). Awh and colleagues therefore developed a framework incorporating past selection history with existing models, leading to an integrated priority map for attentional control (Awh, Belopolsky, & Theeuwes, 2012).

In line with the selection history component described in the model of Awh et al. (2012), behavioral research has shown attentional orienting to the location of a non-salient cue that had acquired value through reward learning (Failing & Theeuwes, 2014). Similarly, eye movements have been observed to land closer to high compared to low reward-signaling distractors (Bucker, Silvis, Donk, & Theeuwes, 2015; McCoy & Theeuwes, 2016). It has recently been suggested that reward learning of particular locations relies upon spatial priority maps, specifically when multiple potential targets compete for attention (Chelazzi et al., 2014). In the study of Chelazzi and colleagues, locations in space were first trained with reward associations, i.e. responding to a target at a particular location consistently led to a high chance of high reward. In a subsequent test phase, letter or digit targets appeared at one, two or none of the possible spatial locations, with distractor non-alphanumeric characters at the remaining locations, and participants had to detect and identify the target alphanumeric stimuli. A competitive advantage was found for targets presented in spatial locations previously associated with high compared to low reward. Participants could also correctly report two targets more often when the targets appeared in opposite visual hemifields, supporting previous findings that the two hemispheres can process information in parallel (Alvarez & Cavanagh, 2005; Luck, Hillyard, Mangun, & Gazzaniga, 1989; Sereno & Kosslyn, 1991). Mutual inhibition between hemifields is assumed to be less than within hemifield, due to less overlap of neuronal receptive fields for stimuli presented in different hemifields (Hickey & Theeuwes, 2011; Mounts & Gavett, 2004). The competitive integration model of saccade programming further suggests that stimuli placed closer together within the visual field lead to combined and integrated saccade activation centered at a location between these two

stimuli (Godijn & Theeuwes, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001).

Other studies examining the effects of spatial-based reward on covert attention have reported a decrease in manual response time to targets presented at a previously rewarded location (Hickey, Chelazzi, & Theeuwes, 2014; Stankevich & Geng, 2014). However, very little research has been carried out in humans on how location-specific reward affects eye movements to those locations, or on how location-based reward mechanisms might transfer from overt to covert attention. In one relevant study different groups of participants had to perform a task that required overt responses in one group or covert responses in the other group (Camara, Manohar, & Husain, 2013). The results showed similar reward effects across the two groups, namely that when a particular location was associated with high compared to low monetary reward (training phase), participants later freely choose the location that had previously been more often associated with the high reward. They also found that distractors captured gaze (overt group) or increased errors (covert group) more when they appeared at the high compared to low reward location in the subsequent test phase. Although this study shows similar influences across the two attentional domains, individual participants always used the same response mode in both phases, with no within-participant transfer across attentional settings. Thus, it does not provide insight into how an individual’s learning of location-based reward translates from overt to covert attention.

The present study was therefore designed to investigate whether and how reward associations based on spatial location translate from overt eye movements to covert attention within individual participants. We hypothesized that if reward associations can indeed be tied to different locations in space, and if overt and covert attentional orienting depend on overlapping neuronal populations, representing the integration of exogenous, endogenous and reward-related factors, then both overt and covert attentional measures should display similar spatial-based reward learning. Specifically, we expected this to be evident by reduced saccade latency and manual reaction time (RT) to stimuli presented at locations associated with higher reward value. Due to previous research on the effect of visual hemifield, we designed the experiment to maximally separate attentional allocation towards the high and low reward locations by placing them in opposite visual hemifields. In this way, attention to rewarded locations should not be influenced by strong within-hemifield integration or inhibition, and the outcome can be assumed to be driven by the absolute reward value at a given location. We tested our hypotheses using two different task contexts: one learning phase in which saccades were made towards a salient stimulus presented at locations associated with high, low, or no reward, and one pre-training baseline and post-training test phase in which participants fixated at the center and carried out a covert visual discrimination task with stimuli presented at these same locations. The only consistent parameter across tasks in this experiment was the relative spatial positions of the stimuli, i.e., all stimulus features were different across tasks. In this way, we wished to determine the entirely spatial nature of reward learning across the two types of attentional orienting.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Twenty-four participants (9 female; mean 23.6 ± 3.1 years old) with normal or corrected-to-normal vision gave written informed consent to take part in the study. The experiment was approved by the Scientific and Ethical Review Committee of the VU University Amsterdam and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Participants

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