

# Common Priority Map for Selection History, Reward and Emotion in the Oculomotor System

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## Abstract

In natural scenes, many objects compete for visual selection. However, it is not always clear why certain objects win this competition. I will demonstrate that the eye movement system lives in a constant state of competition among different oculomotor programs. This competition is not limited to the competition between the current goals of the observer and salient objects in the environment but incorporates independent influences from memory, reward, and emotional systems. These involuntary and automatic biases often overcome the goal-directed selection and expose severe limits in goal-driven control. There is also a striking similarity in the way that these very different sources of bias activate the oculomotor system and compete for representation. The inputs from various information sources are integrated in the common map in the oculomotor system for the sole purpose of improving the efficiency of oculomotor selection.

## Keywords

visual attention, eye movements, selection history, reward, emotion, threat-conditioning

In natural scenes, many objects compete for visual selection. However, it is not always clear why certain objects win this competition. People usually find comfort in a thought that visual selection can be accomplished completely according to their current goals or “free will.” This probably comes from the fact that most of the time we eventually reach our current goals. For example, when grocery shopping we can select the brand of potato chips on the shopping list from a large variety of chips sold at the shop. However, everyone has experienced being distracted from this task, for example, by a loud noise of somebody dropping a bottle of wine. Traditionally, attentional control has been conceptualized as a dichotomy: Attention can either be directed in line with one’s current goals (i.e., top-down control) or be driven by

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the physical properties of the environment (i.e., bottom-up control). Recently, it has been suggested that this dichotomy fails to account for a growing number of cases in which selection does not rely on physical salience and is carried out without or even in contradiction to current goals of the observer (Awh, Belopolsky, & Theeuwes, 2012). In the present article, I will describe and compare several of such involuntary biases, such as selection history, reward history, and emotional history from the active vision perspective. This perspective has already proven useful for understanding the interactions between goal-driven and bottom-up control of visual selection. I will propose that the inputs from these various information sources are integrated in the common priority map for the sole purpose of improving the efficiency of oculomotor selection.

## Active Vision Perspective

One of the most important aspects of the primate visual system is that in order to examine the world around us, we have to make fast ballistic eye movements called saccades. Saccades are necessary to quickly bring the fovea, the part of the retina with the highest acuity, to different parts of visual scene. Scanning visual environments is the activity ubiquitous to all aspects of our everyday life. Already in the 1960s, a Russian scientist Alfred L. Yarbus demonstrated that these eye movements are not made at random but instead reflect information processing unfolding in time (Yarbus, Haigh, & Riggs, 1967). In his pioneer and internationally renowned work, he demonstrated that presenting observers with different viewing instructions dramatically changed the way they scanned the same exact artwork. The eye movement patterns reflected the active process of extracting information from the environment. Our vision can, therefore, be viewed as an active process in which the eyes serve as the first filter of visual information into the brain (Findlay & Gilchrist, 2003).

The active vision perspective is in contrast with the widely prevalent view which emphasizes that information can also be extracted covertly, that is, without eye movements (Posner, 1980). According to this view, covert attention constitutes a process of allocating processing resources to different aspects of the environment independently of eye movements. However, the mere fact that it is possible to attend somewhere while holding the eyes still does not mean that covert attention is an independent process. Many studies have demonstrated that there is a close and obligatory coupling between covert attention and saccadic eye movements. Specifically, it has been shown that every saccade is preceded by a shift of visual attention to the saccade goal (e.g., Deubel & Schneider, 1996). Furthermore, every shift of attention is associated with saccade preparation (Belopolsky & Theeuwes, 2009, 2012). Covert attention also affects trajectories of eye movements, making the eyes curve toward or away from attended locations, suggesting that they are coded on the saccade map (McSorley, Haggard, & Walker, 2006). Neurophysiological studies have convincingly demonstrated that the effects of covert attention on visual processing could be mimicked by subthreshold stimulation of saccade-related brain areas, such as frontal eye fields (FEF; Moore & Fallah, 2004). Finally, the eyes are never still. The microsaccades that are made during covert attention tasks have also been shown to reflect allocation of covert attention (Laubrock, Engbert, & Kliegl, 2005). In fact, the movement of the image on the retina is crucial for visual perception. When the image on the retina is stabilized (e.g., Yarbus developed a method that involved placing an image on a suction cup mounted directly on the eyeball), the visual percept quickly fades away.

The evidence suggests that covert attention is not independent from overt attention, but instead should be viewed as an intrinsic part of the eye movement act. According to the influential premotor theory, attention has emerged as an unavoidable consequence of

movement planning (Rizzolatti, Riggio, Dascola, & Umilta, 1987). As noted above, the eyes serve as the first filter of visual information. The fact that overt attention is a serial process allows us to examine how different types of information compete for visual selection. This has already proven to be a fruitful avenue for understanding the competition between physically salient events in the environment and current goals of the observer.

## **Competition Between Physical Salience and Current Goals in the Oculomotor System**

Yarbus has already pointed out that voluntary control of the eye movement system is very limited (Yarbus et al., 1967). He compared the act of looking to the act of walking:

when we have learned how to walk, we no longer think how we must move our legs, – we just walk; when we have learned how to see, we do not think in which order we must fixate – we just look.”

Yarbus noted in his observations that even large amplitude saccades often occur involuntarily and escape our awareness. Recent studies confirmed these observations. For example, in the oculomotor capture task, participants were asked to make a single saccade to a uniquely colored gray circle (Theeuwes, Kramer, Hahn, & Irwin, 1998). Simultaneously with presentation of the target, a new distractor was added to the display with an abrupt onset. On about 30% to 40% of all trials, the eyes first went into the direction of the abrupt onset distractor before turning back and landing on the target. This suggests that task-irrelevant but salient stimuli can win the competition for oculomotor selection. Interestingly, participants were not aware of the fact that their eyes first went in the wrong direction, even when it meant going in the direction opposite from the target location. In fact, such oculomotor errors occurring without awareness have been shown to evoke the error-related negativity—an event-related potential (ERP) component which is generated in the anterior cingulate cortex and is thought to reflect competition between concurrent motor programs (Belopolsky & Kramer, 2006; Belopolsky, Kramer, & Theeuwes, 2008).

Although physical salience and voluntary control have independent inputs into the oculomotor system, they do not lead to two independent oculomotor programs racing against each other (Godijn & Theeuwes, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001). Instead, several findings point toward integration of the two competing programs. For example, when the abrupt onset distractor and the target appear in a close proximity to each other, saccades tend to land at the intermediate locations (Godijn & Theeuwes, 2002). Other studies have consistently demonstrated that the presence of a salient distractor makes saccade curve either toward or away from the distractor location (McSorley et al., 2006; Sheliga, Riggio, & Rizzolatti, 1995). Saccade curvature has been attributed to competition in the oculomotor map for potential saccade targets located in the intermediate layers of superior colliculus (SC; McPeck, Han, & Keller, 2003; Sparks & Hartwich-Young, 1989). Interestingly, the competition between the current goals and salient stimuli does not seem to be constant over time. The direction of saccade curvature seems to reflect the status of competition between the target and distractor oculomotor programs (McSorley et al., 2006). When the neural representation of the distractor is active at the time of eye movement, saccade trajectory tends to curve toward the distractor location. However, resolving the competition at the time of eye movement leads to saccade trajectory curving away from the distractor location. Saccade trajectory deviation away is typically explained by inhibition of the oculomotor program evoked by a visible distractor, which disturbs the overall activation in SC and shifts the saccade vector away from the distractor location

(Aizawa & Wurtz, 1998; Doyle & Walker, 2001; Sheliga et al., 1995; but see Wang, Kruijne, & Theeuwes, 2012).

The results described above suggest that physical salience and current goals are dynamically and competitively integrated on a common priority map in the oculomotor system. It has been proposed that such a map is located in the SC because it represents the latest stage of oculomotor programming and integrates multiple inputs (Findlay & Walker, 1999; Godijn & Theeuwes, 2002; Trappenberg et al., 2001). Below I will review recent evidence suggesting that selection history, reward history, and emotional history also generate activity at the oculomotor priority map and compete for oculomotor selection.

## **Selection History Representations in the Oculomotor System**

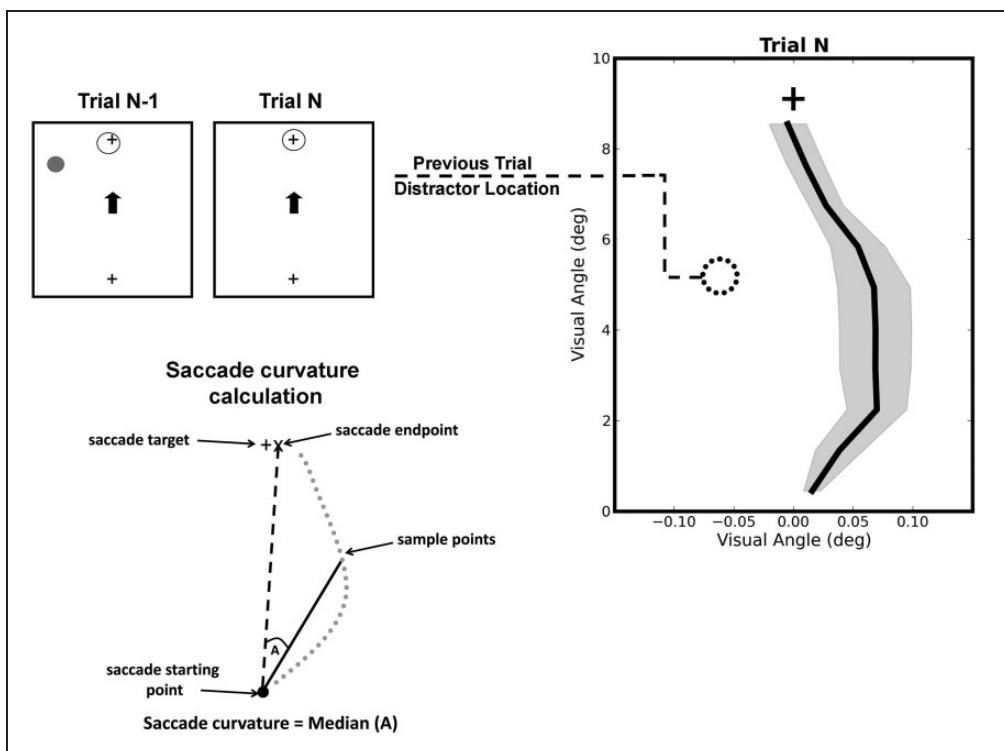
It has been known for some time that previously selected stimuli have the ability to automatically guide visual attention. One classic demonstration of this is the “priming of pop-out” effect, first reported by Maljkovic and Nakayama (1994). They showed that when participants searched for a red diamond, on subsequent trials search was more efficient when the target was repeated. This was the case even when the repetition happened eight trials later. Importantly, this intertrial priming effect did not change even when the observers were made aware that the targets were switching in a completely predictable sequence and thus could prepare for the upcoming target, suggesting that priming can dominate voluntary control.

These experiments have clearly demonstrated that intertrial priming represents a form of short-term implicit memory, responsible for efficient guidance of visual attention. According to the priming account recent selection, history automatically and implicitly biases future selection (Maljkovic & Nakayama, 2000). Based on the previous selection experience, target properties receive more weight on the priority map, while distractor properties receive less weight (Bichot & Schall, 2002). It has been suggested that on the neural level, previous experience with selecting a target results in “sharpening” of its cortical representation and makes it more salient (Desimone, 1996). The intertrial priming has been observed for features as well as locations of both targets and distractors (Lamy, Antebi, Aviani, & Carmel, 2008; Maljkovic & Nakayama, 1994, 1996). This implies that selecting a red target object at a certain location on a current trial biases subsequent selection of red objects, as well as other objects occurring at the previous target location. Similarly, rejecting a red distractor object at a certain location on a current trial biases against subsequent selection of red objects, as well as other objects occurring at the previous distractor location. The fact that selection history is clearly different from physical salience and can dominate the current goals of the observer suggests that it constitutes a separate form of control (Awh et al., 2012).

Importantly, several studies have demonstrated that the priority generated by selection history is communicated to the oculomotor map and competes with current goals. For example, McPeck and colleagues (McPeck, Maljkovic, & Nakayama, 1999; McPeck, Skavenski, & Nakayama, 2000) have elegantly demonstrated the intertrial priming for target feature using saccadic eye movements (see also Becker, 2008). In their experiment, which was based on the priming of pop-out task, they asked participants to make a single saccade to a color singleton target. Search displays could contain either a red diamond among green diamonds, or a green diamond among red diamonds. The authors showed saccade latencies to the color singleton targets were shorter if on recent trials targets happened to have the same color as on the current trial (McPeck et al., 1999). However, saccades also frequently (30% of the trials) tended to erroneously go in the direction of the distractors with the same color as the target on the previous trial (McPeck et al., 2000). Some

of these saccades landed on the distractors, while others only curved toward them and were redirected to the target in midflight.

A recent study extended these findings to intertrial priming of distractor locations (Belopolsky & Van der Stigchel, 2013). Specifically, by measuring saccade curvature, the authors examined how previous competition between target and distractors is represented in the oculomotor system. Participants performed a simple task of making a saccade toward a predefined direction (Figure 1). On two thirds of the trials, an irrelevant distractor was presented either to the left or to the right of the fixation. On one third of the trials, no distractor was present. The results showed that on trials without a distractor, saccades curved away from the empty location that was occupied by a distractor on the previous trial. Repetition of distractor location on the distractor present trials also led to a stronger curvature away. Note that the distractor was completely irrelevant to the task and participants did not have to actively maintain its location in memory. Nevertheless, its memory trace clearly competed for representation in the oculomotor system. These results were taken as the evidence that the oculomotor system automatically codes and retains



**Figure 1.** Intertrial priming of distractor location as measured by saccade curvature in the study by Belopolsky and Van der Stigchel (2013). Participants were asked to make a saccade in the direction of a central arrow which was always pointing in the same direction (up or down) for a given participant. In two thirds of the trials, a distractor was presented simultaneously with the target and occurred unpredictably in the left or right hemifield. On the rest of the trials, no distractor was present. The open circle was not present in the actual display and indicates where participants had to fixate during the trial. On the distractor absent trials saccades curved away from the locations where distractor had been presented on the previous trial. Adapted with permission from Belopolsky and Van der Stigchel (2013).

locations that had been ignored in the past in order to bias future behavior. The absence of a distractor did not mean that there was no competition on that trial—this suggests that the oculomotor system lives in a constant state of competition that extends beyond current stimulation.

It has been proposed that selection history represents the automatic implicit memory system that is especially well suited for rapid attentional guidance required by the saccadic system (McPeck et al., 1999). Given that, we make about 170,000 saccade every waking day, there is a need for a system that can quickly and accurately guide our oculomotor selection and does not require additional cognitive resources.

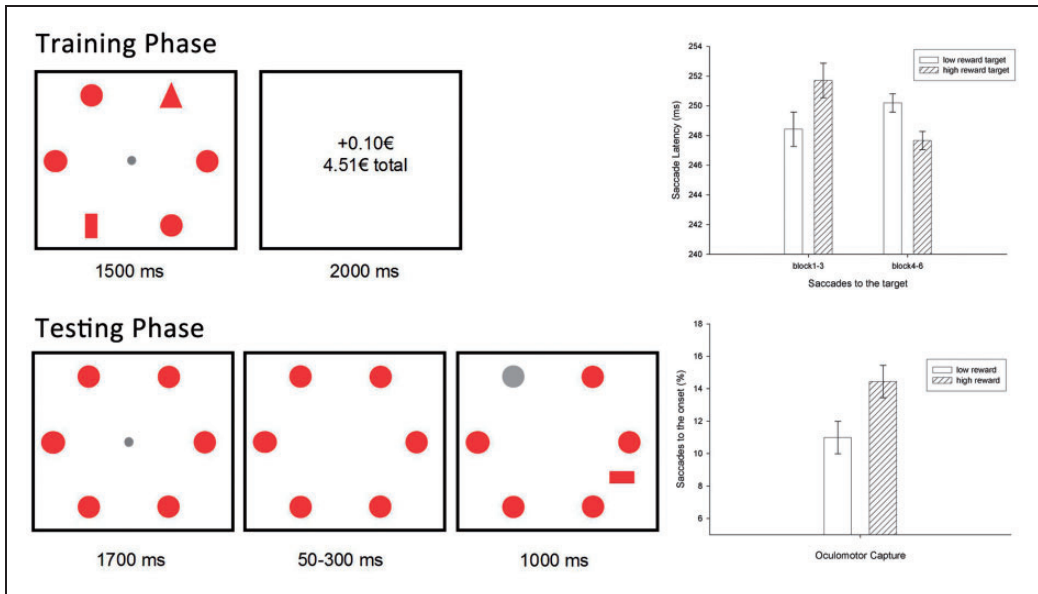
## Reward History Representations in the Oculomotor System

Recent studies have demonstrated that stimuli previously associated with monetary reward have the ability to capture attention despite the current goals and independently of physical salience. For example, in the study by Anderson, Laurent, and Yantis (2011), participants had to search for either a red or green target. After a correct response, observers received a monetary reward, which was linked to the color of the target, such that one of the two colors was associated with a high and the other with a low reward. In the test phase, participants no longer received reward but had to search for a unique shape while a color distractor was presented on some trials. The results showed that the colored distractor previously associated with a high monetary reward caused significantly more distraction as evidenced by an increased time to find the target than a color singleton that was associated with a low monetary reward. It was proposed that reward changes the salience of a stimulus such that a stimulus that is associated with high reward receives attentional priority independent of strategic control (for a review, see Anderson, 2013).

A few studies have looked at whether previously rewarded stimuli also generate activity in the oculomotor system and compete for the oculomotor selection. For example, Anderson and Yantis (2012) did not constrain participants' eye movements and showed that participants were spontaneously biased to fixate more often the side of the display that contained a previously rewarded distractor. However, inconsistent with previous studies using covert attention (Anderson et al., 2011), the value of previous reward (i.e., high or low reward) did not have any effect on the oculomotor selection. Theeuwes and Belopolsky (2012) used the oculomotor capture task in which participants had a clear goal of making a saccade to a color singleton (Figure 2). On half of the trials, an abrupt onset distractor appeared, and its orientation was associated either with high or low reward in a preceding training session. The results clearly showed that the task-irrelevant onset that was previously associated with high monetary reward captured the eyes much stronger than that very same stimulus when previously associated with low monetary reward. Interestingly, there was no effect on fixation duration on the distractor, suggesting that reward affected only initial overt selection and not the disengagement processes (Born, Kerzel, & Theeuwes, 2011). The authors argued that reward changes the salience of a stimulus and directly bias the oculomotor selection according to the actually learned reward value.

The presence of a distractor previously associated with high reward did not slow down the saccade latency to the target relative to the presence of a distractor previously associated with low reward. Note that this difference was expected if the information about reward value were competitively integrated on the saccade map (Godijn & Theeuwes, 2002). One possibility is that object's association with high-reward value gives an independent boost to the saccade program to its location. This biases the competition in its favor without affecting the integration on the saccade priority map.





**Figure 2.** Previously rewarded stimuli capture the eyes even when completely irrelevant to the task (Theeuwes & Belopolsky, 2012). In the training phase, participants had to make an eye movement either to a horizontal or a vertical bar. One of the bars was associated with high reward and the other with low reward. In the test phase, the onset distractor that was associated with a high monetary reward during the training phase captured the eyes more often than the onset distractor that was associated with a low monetary reward. Adapted with permission from Theeuwes and Belopolsky (2012).

Reward has also been shown to influence saccade trajectories. For example, in a study by Hickey and van Zoest (2012), participants had to make a saccade to a target presented either up or down from fixation and to ignore a distractor presented to the left or right of fixation. The colors of target and distractor could swap randomly from trial to trial, and a random high or low reward was given on the correct trials. The results showed that for short-latency saccades, the eyes deviated more toward the distractors which color was coupled with high reward on the previous trial, while for the long-latency saccades the eyes deviated more away from these distractors. This suggests that reward association on the previous trial exerts direct competition in the oculomotor system.

The effects of reward on oculomotor selection have been demonstrated even in situations in which attending to the stimuli that signal reward was counterproductive. To that end, Le Pelley, Pearson, Griffiths, and Beesley (2015) used the oculomotor capture task, in which the color of the distractor conveyed the reward value available for that trial. Importantly, the availability of reward was dependent on very fast saccades to the target. Nevertheless, participants' eyes were captured by the distractors predicting reward for selecting the target and more so by the high than low-reward distractors. Confirming this finding, a recent study showed that saccade landing position was also biased in the direction of distractor predicting the possibility of high reward (Bucker, Belopolsky, & Theeuwes, 2014). This implies that information about impending reward is an extremely potent force that disrupts goal-directed oculomotor behavior.

Taken together the findings described above suggest that stimuli previously associated with reward or predicting reward availability have a strong and automatic representation

in the oculomotor system. This is consistent with the idea that the reward system in the brain promotes approach behavior in order to maximize positive outcomes (Berridge & Robinson, 1998). Importantly, the oculomotor bias toward stimuli that have delivered positive outcomes in the past seems to occur automatically and strongly competes with current selection goals.

## Emotion Representations in the Oculomotor System

Many studies suggested that emotional information, especially the information related to danger is also prioritized by the visual system because of its behavioral significance (for a review, see Pessoa & Adolphs, 2010). From an evolutionary perspective, fear may have evolved as anticipation of an aversive outcome, which allows an organism to execute or inhibit appropriate overt behavior (Lang, Davis, & Öhman, 2000). Fast identification of threat-related cues may, therefore, give an evolutionary advantage and improve chances of survival (LeDoux, 1998). For example, one recent study used classical conditioning procedure to associate a certain color with a possibility of receiving an electric shock (Schmidt, Belopolsky, & Theeuwes, 2014a). Following such fear-conditioning participants completed a visual search task in which the stimulus associated with fear could appear as a distractor. The results showed that the presence of an irrelevant distractor that was previously associated with fear slowed search more than a distractor without fear association. It was concluded that learned fear associations have the ability to capture our attention despite the current goals.

Several previous studies have demonstrated that stimuli associated with threat influence oculomotor selection even when they are not in line with current goals. For example, Nummenmaa, Hyönä, and Calvo (2009) have asked participants to make an eye movement to one of the two scenes indicated by the central cue. One of the scenes had an emotional content (positive or threatening) and the other one was emotionally neutral, while the cue was equally likely to point to either one. The results showed that participants were faster in making saccades to the emotional scene when it happened to be the saccade goal and made more erroneous eye movements toward the emotional scene when it was a distractor. In a follow-up experiment, they showed that vertical saccades tended to curve away from the location of the emotional scene, suggesting that it directly competed for representation in the oculomotor system. More recent studies have proposed that stimuli associated with threat are especially potent and fast in biasing the oculomotor selection. For example, Schmidt and coworkers (Schmidt, Belopolsky, & Theeuwes 2012) showed that the eyes curved away from the locations that happened to be occupied by angry faces, although they were completely irrelevant for the task at hand (see also Petrova & Wentura, 2012). No such effect was observed for happy faces.

One difficulty of studying effects of emotional information upon visual selection has to do with profound physical differences between the stimuli conveying different emotions, as well as emotionally neutral stimuli. To overcome this, potential confound researchers have used threat-conditioning approach, in which physically identical abstract features (colors, shapes, etc.) were first associated with an unpleasant stimulus. Mulckhuyse, Crombez, and Van der Stigchel (2013) demonstrated that stimuli that were first associated with an unpleasant sound using classical conditioning influence saccade trajectories in the subsequent test session. Specifically, the short-latency saccades tended to curve toward the fear-conditioned distractor, while the long-latency saccades curved away from their location.

Interestingly, a recent study used the exact design of the oculomotor capture reward task of Theeuwes and Belopolsky (2012), but instead of giving high or low reward, the authors conditioned a certain orientation to be associated with a high or low probability of receiving



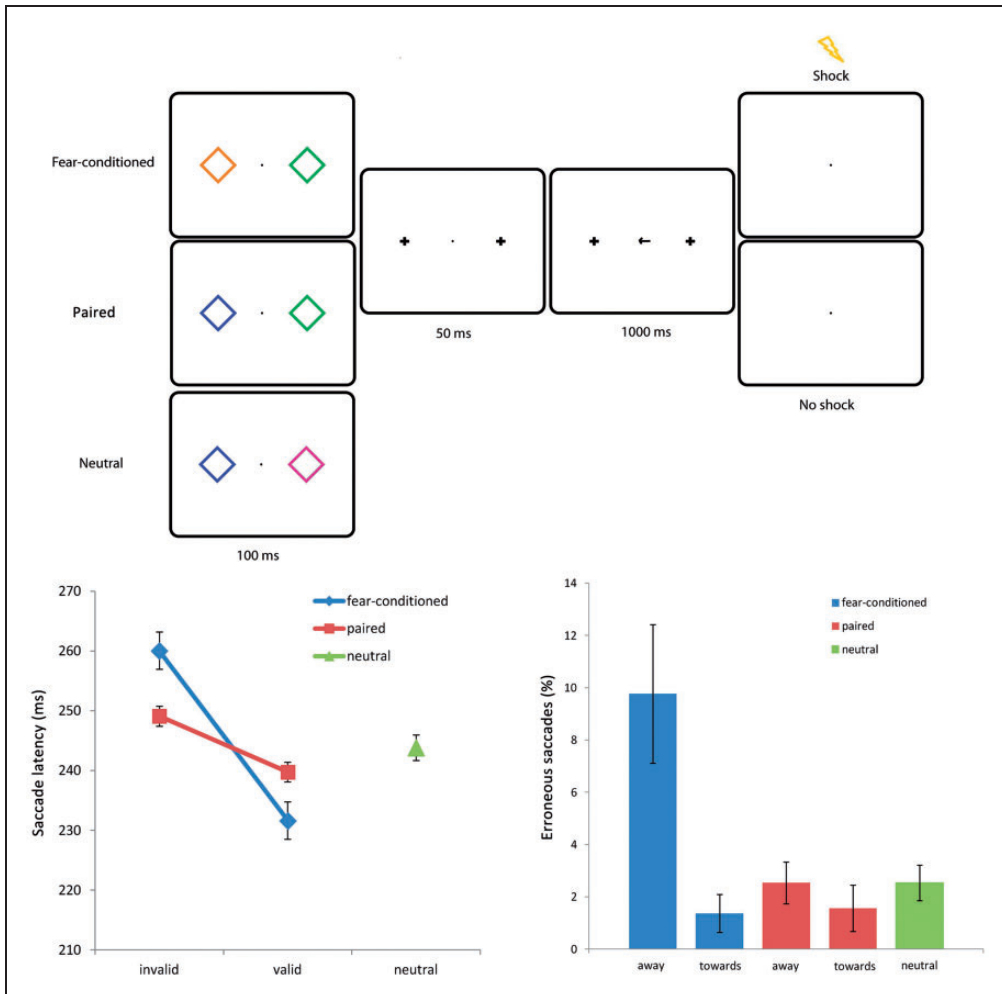
an electrical shock (Hopkins, Helmstetter, & Hannula, 2014). There was a striking resemblance to the results of Theeuwes and Belopolsky (2012). During the oculomotor capture task, which did not involve any shocks, the onset distractors that were previously associated with a high probability of shock captured the eyes more often than the stimuli that were associated with a low probability of shock. There was also no effect on fixation durations, suggesting that just as reward, threat did not affect the disengagement processes in this task. Finally, just as in the case of rewarded stimuli in the study by Theeuwes and Belopolsky (2012), the presence of a distractor previously associated with high probability of shock did not slow down the saccade latency to the target relative to the presence of a distractor previously associated with low probability of shock. It is possible that reward and threat-conditioning both operate by biasing the competition in their favor without affecting the integration on the oculomotor priority map.

Studies that used threat-conditioning typically find that the effects of conditioning dissipate quickly with time. The short life cycle of these biases can be seen as adaptive: It is important not to discard previous predictors of threat too quickly, at least not until the context has changed. It would be maladaptive to keep the biases for a long time and generalize them to every situation, which could lead to formation of phobias (Ohman & Mineka, 2001). To take this issue into account, Schmidt, Belopolsky, and Theeuwes (2014b) presented participants with two stimuli and informed them that the presence of the stimulus with one particular color can lead to the delivery of electrical shock at the end of the trial (Figure 3). This ensured that a genuine threat of shock was presented during the whole experiment. Participants were encouraged to make a speeded saccade to the location indicated by a central cue. The results clearly showed that saccade toward the fear-related stimulus were initiated faster than to the neutral stimuli. Furthermore, saccades often erroneously went into the direction of threat even when saccade to a different location was required.

The evidence described above suggests that stimuli with emotional content and especially the threat-related stimuli evoke a strong and automatic representation in the oculomotor system. They seem to bias the oculomotor selection despite clear voluntary goals. This is consistent with the idea that fear has evolved as a precursor of a negative outcome, which could prepare the organism to take appropriate action. Fast and accurate detection of the cues predicting danger would give an advantage in choosing whether to flee or to fight.

## **Integrating Selection History, Reward and Emotion in the Oculomotor System**

From the evidence presented above, it is clear that competition for visual selection is not limited to the competition between the current goals of the observer and salient objects in the environment but incorporates independent influences from memory, reward, and emotional systems. These involuntary and automatic biases often overcome the goal-directed selection, especially early in time. In general, there is a remarkable similarity between these automatic biases and the bias produced by physically salient stimuli. To summarize, both types of biases produce the oculomotor capture by the distracting stimulus but do not affect the process of disengagement from it. Furthermore, both types of biases affect saccade trajectories to the target with faster saccades curving toward the distractor and slower saccades curving away from the distractor. Finally, close proximity of the distractor to the target results in averaging of activations on the saccade map and saccades landing at the intermediate positions. Together, these results suggest that automatic biases from selection history, reward history, and threat history are competitively integrated on the common priority map, presumably located in the SC. One inconsistent finding so far is that competitive



**Figure 3.** Potentially threatening stimuli that predict electrical shock facilitate eye movements to its location and disrupt execution of voluntary saccades to other locations as evident in saccade latencies and saccade errors (relative to the neutral condition). Additionally, the neutral stimulus that consistently accompanies the threatening stimulus (see the paired condition) shows a similar pattern of costs and benefits when combined with a completely neutral stimulus. The validity effect in the paired condition occurred even though the combination of a paired and a neutral stimulus was in fact never accompanied with a shock. Adapted with permission from Schmidt, Belopolsky, and Theeuwes (2015).

integration of stimuli associated with high reward or high chance of shock was not observed in the saccadic latencies in the oculomotor capture task. One possibility is that this was due to a ceiling effect: The presence of the onset distractor had already slowed down saccade latencies to the target, and the presence of high reward or high chance of shock could not slow down the latencies any further.

The puzzling question is how the selection history, reward, and emotion systems with different underlying neural mechanisms are integrated on the common priority map used by the oculomotor system and presumed to be located in the SC. One way to look at this problem is to step away from the modularity view of brain function (Pessoa, 2008; Pessoa & Adolphs, 2010). As suggested by Pessoa (2008), it is more fruitful to look for integration of

different specialized systems relying on the same large scale neural networks, instead of trying to understand how they interact. In the end, the problem that brain really has to solve is how to select relevant information and to prepare for the appropriate course of action. One possibility is that memory, reward, and emotional systems all feed into the same large attentional network, consisting of several priority maps located in the FEF, in the lateral intraparietal area (LIP) and in the SC.

Consistent with this idea, it has been suggested that in the brain selection history, effects are pervasive throughout the information processing stream and might involve both low-level sensory systems and higher level systems for episodic memory (Kristjánsson & Campana, 2010). It is feasible that areas in the medial temporal lobe, such as hippocampus, are involved in maintenance of selection history for locations. In support of this claim, several studies showed that eye movements of amnesic patients do not show a pattern consistent with the presence of relational memory. Specifically, when presented with a repeated view of the same scene with one region altered, normal participants show increased eye fixations to this altered region without explicit report of the change. This effect is, however, absent in amnesic patients (Ryan, Althoff, Whitlow, & Cohen, 2000). Furthermore, a recent study demonstrated that activity in the hippocampus reliably predicted the probability of making an eye movement to the relational change in the scene in the absence of explicit report (Hannula & Ranganath, 2009). On the other hand, selection history for visual features most likely involves tuning of neural responses in specialized sensory cortices which in turn biases their representation on the priority map, presumably in the LIP.

In contrast to selection history, reward and emotion seem to be processed in more dedicated systems in the brain. Reward processing is thought to be accomplished by a dopaminergic network distributed throughout the brain (Berridge & Robinson, 1998). Single cell recording suggested that reward can have direct influence on the intermediate layers of SC through inputs from basal ganglia and substantia nigra (Ikeda & Hikosaka, 2003). However, both FEF and LIP have also shown modulation by reward expectation and could provide input to the SC (Kobayashi, Lauwereyns, Koizumi, Sakagami, & Hikosaka, 2002; Platt & Glimcher, 1999). Many studies have argued for existence of a direct subcortical pathway through the SC and pulvinar to the amygdala, specialized for processing of emotional information (Vuilleumier, 2005). Such connection would presumably allow fast and nonconscious processing of affective information. Note that the SC only provides coarse visual input to the amygdala but cannot evaluate threat relevance. Therefore, input to the SC depends on the feedback connections from the amygdala. Whether a fast-track connection between the amygdala and cortical structures exists in the human brain is still under debate. In addition, the cortical pathway could also activate the amygdala and provide feedback into the SC almost as quickly (Pessoa & Adolphs, 2010).

## Conclusions

The findings reviewed in this article clearly suggest that the eye movement system lives in a constant state of competition among concurrent oculomotor programs. This competition is not limited to the competition between the current goals of the observer and salient objects in the environment but incorporates independent influences from memory, reward, and emotional systems. These involuntary and automatic biases often disrupt the goal-directed selection, especially during the early stages of competition. Overall, this exposes severe limits in the goal-driven control over the oculomotor selection. There is also a striking similarity in the way that these very different sources of bias activate the oculomotor system and compete for representation. All of these biases support fast and automatic allocation of attention

imposing a very low cognitive load. Moreover, the biases are transient in a sense that they typically persist only over several trials, unless reinforced. This ensures that they are tuned to the constantly changing demands of the environment and the task being performed. All these properties are essential for the purpose of improving the efficiency of oculomotor selection.

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### References

- Aizawa, H., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. I. Curvature of saccadic trajectory. *The Journal of Neurophysiology*, *79*, 2082–2096.
- Anderson, B. A. (2013). A value-driven mechanism of attentional selection. *Journal of Vision*, *13*, 7.
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011). Value-driven attentional capture. *Proceedings of the National Academy of Sciences*, *108*, 10367–10371.
- Anderson, B. A., & Yantis, S. (2012). Value-driven attentional and oculomotor capture during goal-directed, unconstrained viewing. *Attention, Perception, & Psychophysics*, *74*, 1644–1653.
- Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, *16*, 437–443.
- Becker, S. I. (2008). The mechanism of priming: Episodic retrieval or priming of pop-out? *Acta Psychologica*, *127*, 324–339.
- Belopolsky, A. V., & Kramer, A. F. (2006). Error-processing of oculomotor capture. *Brain Research*, *1081*, 171–178.
- Belopolsky, A. V., Kramer, A. F., & Theeuwes, J. (2008). The role of awareness in processing of oculomotor capture: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *20*, 2285–2297.
- Belopolsky, A. V., & Theeuwes, J. (2009). When are attention and saccade preparation dissociated? *Psychological Science*, *20*, 1340–1347.
- Belopolsky, A. V., & Theeuwes, J. (2012). Updating the premotor theory: The allocation of attention is not always accompanied by saccade preparation. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 902.
- Belopolsky, A. V., & Van der Stigchel, S. (2013). Saccades curve away from previously inhibited locations: Evidence for the role of priming in oculomotor competition. *Journal of Neurophysiology*, *110*, 2370–2377.
- Berridge, K. C., & Robinson, T. E. (1998). What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Research Reviews*, *28*, 309–369.
- Bichot, N. P., & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: Feature-based facilitation and location-based inhibition of return. *Journal of Neuroscience*, *22*, 4675–4685.

- Born, S., Kerzel, D., & Theeuwes, J. (2011). Evidence for a dissociation between the control of oculomotor capture and disengagement. *Experimental Brain Research*, *208*, 621–631.
- Bucker, B., Belopolsky, A. V., & Theeuwes, J. (2014). Distractors that signal reward attract the eyes. *Visual Cognition*, *23*, 1–24.
- Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences*, *93*, 13494–13499.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*, 1827–1837. doi:10.1016/0042-6989(95)00294-4
- Doyle, D., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, *139*, 333–344.
- Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision: The psychology of looking and seeing*. Oxford, England: Oxford University Press.
- Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *The Behavioral and Brain Sciences*, *22*, 661–721.
- Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology–Human Perception and Performance*, *28*, 1039–1053.
- Hannula, D. E., & Ranganath, C. (2009). The eyes have it: Hippocampal activity predicts expression of memory in eye movements. *Neuron*, *63*, 592.
- Hickey, C., & van Zoest, W. (2012). Reward creates oculomotor salience. *Current Biology*, *22*, R219–R220.
- Hopkins, L. S., Helmstetter, F. J., & Hannula, D. E. (2014). Oculomotor capture by aversive stimuli in the absence of contingency knowledge. Presented at the annual meeting of Psychonomic Society, Long Beach, CA.
- Ikeda, T., & Hikosaka, O. (2003). Reward-dependent gain and bias of visual responses in primate superior colliculus. *Neuron*, *39*, 693–700.
- Kobayashi, S., Lauwereyns, J., Koizumi, M., Sakagami, M., & Hikosaka, O. (2002). Influence of reward expectation on visuospatial processing in macaque lateral prefrontal cortex. *Journal of Neurophysiology*, *87*, 1488–1498.
- Kristjánsson, Á., & Campana, G. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, & Psychophysics*, *72*, 5–18.
- Lamy, D., Antebi, C., Aviani, N., & Carmel, T. (2008). Priming of pop-out provides reliable measures of target activation and distractor inhibition in selective attention. *Vision Research*, *48*, 30–41.
- Lang, P. J., Davis, M., & Öhman, A. (2000). Fear and anxiety: Animal models and human cognitive psychophysiology. *Journal of Affective Disorders*, *61*, 137–159.
- Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Research*, *45*, 721–730.
- LeDoux, J. (1998). *The emotional brain: The mysterious underpinnings of emotional life*. New York, NY: Simon and Schuster.
- Le Pelley, M. E., Pearson, D., Griffiths, O., & Beesley, T. (2015). When goals conflict with values: Counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General*, *144*, 158–171.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, *22*, 657–672.
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, *58*, 977–991.
- Maljkovic, V., & Nakayama, K. (2000). Priming of popout: III. A short-term implicit memory system beneficial for rapid target selection. *Visual Cognition*, *7*, 571–595.
- McPeck, R. M., Han, J. H., & Keller, E. L. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology*, *89*, 2577–2590.
- McPeck, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, *39*, 1555–1566.

- McPeck, R. M., Skavenski, A. A., & Nakayama, K. (2000). Concurrent processing of saccades in visual search. *Vision Research*, *40*, 2499–2516.
- McSorley, E., Haggard, P., & Walker, R. (2006). Time course of oculomotor inhibition revealed by saccade trajectory modulation. *Journal of Neurophysiology*, *96*, 1420–1424.
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*, 152–162.
- Mulckhuyse, M., Crombez, G., & Van der Stigchel, S. (2013). Conditioned fear modulates visual selection. *Emotion*, *13*, 529.
- Nummenmaa, L., Hyönä, J., & Calvo, M. G. (2009). Emotional scene content drives the saccade generation system reflexively. *Journal of Experimental Psychology: Human Perception and Performance*, *35*, 305.
- Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483–522.
- Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, *9*, 148–158.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a ‘low road’ to ‘many roads’ of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773–783.
- Petrova, K., & Wentura, D. (2012). Upper–lower visual field asymmetries in oculomotor inhibition of emotional distractors. *Vision Research*, *62*, 209–219.
- Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, *400*, 233–238.
- Posner, M. I. (1980). Orienting of attention, the VIIth Sir Frederic Bartlett Lecture. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 3–25.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40.
- Ryan, J. D., Althoff, R. R., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, *11*, 454–461.
- Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2012). The presence of threat affects saccade trajectories. *Visual Cognition*, *20*, 284–299.
- Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2014a). Attentional capture by signals of threat. *Cognition and Emotion*, *29*, 687–694.
- Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2014b). Potential threat attracts attention and interferes with voluntary saccades. *American Psychological Association*, *15*, 329–338.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research*, *105*, 261–75.
- Sparks, D. L., & Hartwich-Young, R. (1989). The deeper layers of the superior colliculus. In R. H. Wurtz, & M. E. Goldberg (Eds.), *Rev. Oculomotor Res., The Neurobiology of Saccadic Eye Movements* (pp. 213–255). Amsterdam, the Netherlands: Elsevier Science Publishers.
- Theeuwes, J., & Belopolsky, A. V. (2012). Reward grabs the eye: Oculomotor capture by rewarding stimuli. *Vision Research*, *74*, 80–85.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of eyes by new objects. *Psychological Science*, *9*, 379–385.
- Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, *13*, 256–271.
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*, 585–594.
- Wang, Z., Kruijine, W., & Theeuwes, J. (2012). Lateral interactions in the superior colliculus produce saccade deviation in a neural field model. *Vision Research*, *62*, 66–74.
- Yarbus, A. L., Haigh, B., & Riggs, L. A. (1967). *Eye movements and vision* (Vol. 2). New York, NY: Plenum press.