of the population (which is now an evolutionary response).

***Wouldn't that be a good way of studying evolution in action over a few generations?*** One would think so. In particular, it is possible to measure all three components of the breeder's equation, and see directly whether $R = h^2S$. But, quite often, it appears that $R$ does not equal $h^2S$. For example, a study on antler size in red deer showed that red deer with larger antlers had more offspring than red deer with smaller antlers, and antler size has a high heritability. Yet no response to selection, $R$, could be detected. How is this possible? The problem is not in the measurement of $h^2$ or $R$, but in the measurement of $S$. In artificial selection, where individuals are selected by the experimenter on the basis of their value of the trait, it is the trait itself that determines reproduction, and any source of variation in the trait will affect which individuals are chosen. But, in studies of natural selection, all that is seen is a correlation between measured fitness and the trait. In this case, therefore, the trait itself does not necessarily cause the fitness differences. An environmental insult, such as disease, could simultaneously lower the trait value and also survivorship and/or reproduction, in other words, fitness. The consequence is that it is possible to have a trait–fitness correlation, arising from a purely environmental covariance, which creates the false impression of selection, without there being any correlation between fitness and the breeding value of the trait. What matters is the genetic correlation between fitness and the trait.

### *Where can I find out more?*

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Centre for Genetics and Genomics, School of Biology, University of Nottingham, University Park, Nottingham NG7 2RD, UK.
E-mail: john.brookfield@nottingham.ac.uk

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## Correspondence

# Reward creates oculomotor salience

**Clayton Hickey[1,2]**
**and Wieske van Zoest[1,2]**

Theories of animal approach behaviour suggest that reward can create low-level biases in perceptual and motor systems, potentiating the processing of reward-associated environmental stimuli and causing animals to instinctively orient the head and eyes toward these objects [1]. However, the idea that reward can have this kind of direct impact on subsequent oculomotor processing has never been robustly tested, and existing research has largely confounded low-level effects with those mediated by strategy and attentional-set [2]. Here we demonstrate in humans that saccade trajectories are disrupted by a reward-associated distractor even when participants expect this object, know where it may appear, and do their best to ignore it. The reward history of a visual object thus has a direct, low-level, and non-strategic influence on how we deploy our eyes.

Prior research on the role of reward in oculomotor programming has largely relied on experimental designs in which neural or oculomotor responses to reward-predictive stimuli are examined [3]. This type of design does not allow for the distinction between a direct impact of reward and an influence mediated by strategy. Humans and other animals tend to look out for objects that provide information about upcoming reward [4], and this kind of attentional set is known to enhance visual and oculomotor responses [5]. Oculomotor bias toward reward-predictive stimuli thus is likely to reflect a strategic, indirect influence of reward feedback, mediated by attention, rather than the low-level, non-strategic priming proposed by theory.

Here we test whether a visual object's reward history has an impact on saccadic trajectory that is independent of strategy, and even in spite of it. We measured eye movements in eighteen healthy humans while they completed a saccadic selection task. This involved orienting the eyes from a central fixation point to a target located at either the top center or bottom center of a computer screen. In every trial a task-irrelevant distractor was presented slightly to the left or right of the direct path between fixation and the target (Figure 1A). The distractor could be red with the target green, or vice versa, and this was randomly determined for each trial. Participants knew that stimuli at the distractor locations must be ignored and that the colors of the target and distractor were task irrelevant.

Prior research with this type of display has shown that the distractor will cause target-directed saccades to deviate from their normal path, curving toward the distractor when the saccade is initiated quickly and away when it occurs later in time [6]. This time-course of deviation is thought to reflect the development of a spatially-specific inhibitory response to distractor salience, and saccadic deviation is accordingly used as a behavioural metric of salience in the oculomotor system [7].

When participants correctly deployed their eyes to the target they received a reward, either 1 or 10 points, with earnings for the experimental session determined by the number of accumulated points. Critically, reward magnitude was random: so long as participants completed the task correctly, they were as equally likely to receive high-magnitude reward as low.

We expected that receipt of high-magnitude reward would potentiate subsequent processing of target features, increasing their relative salience [8]. Accordingly, when high-magnitude reward was received and the target and distractor colors swapped between trials, the distractor — now characterized by the color that defined the rewarding target in the immediately preceding trial — would have a stronger impact on the target-directed saccade. Trials were therefore binned based on two orthogonal experimental dimensions: whether the immediately preceding trial had garnered high or low-magnitude reward, and whether the target and distractor colors had swapped between trials (Figure 1A). We also separated trials into short latency, mid latency, and long latency conditions, reflecting the speed with which the saccade was initiated after

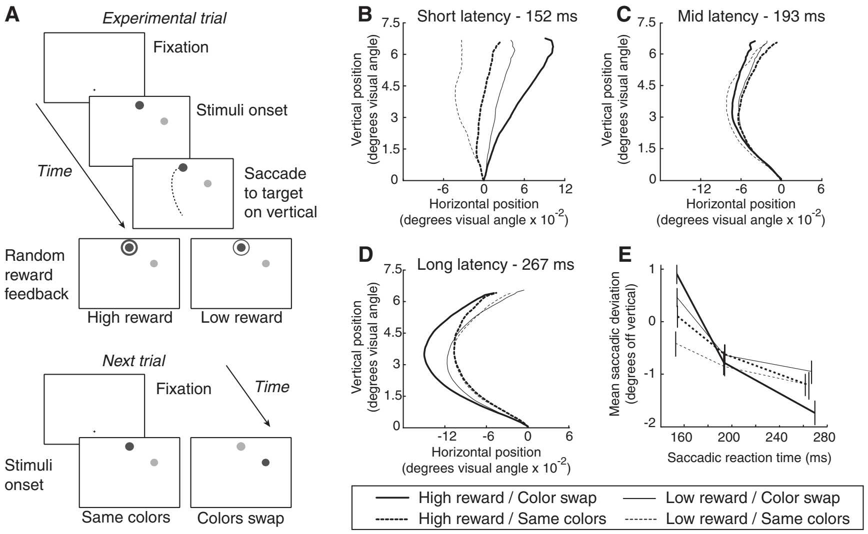

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Figure 1. Experimental paradigm and results.

(A) Paradigm schematic. Target and distractor could be presented in red or green color; these differences in color are denoted here by shading. (B) Short latency, (C) mid latency, and (D) long latency saccadic trajectories, with horizontal scale magnified. These plots are in reference to a target in the upper hemifield and distractor in the right upper quadrant. (E) Mean angular deviation from a direct path between fixation and target for each condition and latency bin. Positive saccadic deviation values on the y-axis indicate curvature toward the distractor. Error bars reflect within-subject 95% confidence intervals.

stimulus onset (for details see the Supplemental Information available on-line with this issue).

Figures 1B–D illustrate the saccadic deviation observed per experimental condition in each of the latency bins. Targets could be in the upper or lower visual hemifield, and distractors to the left or right, but these rectified plots are collapsed across stimuli locations and are in reference to a target in the upper hemifield and distractor in the right upper quadrant.

Short latency target-directed saccades in the high-reward/color swap condition (illustrated by the thick solid line in Figure 1B) are clearly drawn more closely to the distractor than saccades in the high-reward/same colors condition ($P = 0.029$). In contrast, long latency target-directed saccades (illustrated by the thick solid line in Figure 1D) clearly deviate further away ($P = 0.036$). For the purposes of numeric and statistical analysis we calculated a metric of saccade eccentricity based on mean angular deviation from a straight path between fixation and target [6]. These values are illustrated in Figure 1E and reiterate the pattern (see Supplemental Information for extended statistics).

Further analysis revealed: that the eyes were more likely to be erroneously deployed to the distractor location in the high-reward/swap condition than in the other conditions (3.6% vs. 2.5% of total eye movements); that target selection was less accurate in the high-reward/swap condition than in other conditions when saccades were quickly initiated, but became better when time passed between stimulus onset and saccadic execution; and that saccadic flight time was consistently longer in the high-reward/swap condition (Supplemental Figures S1A,E,F and Supplemental Results). A control experiment verified that the data pattern was created by the value of feedback stimuli, not physical differences in ring size (Supplemental Discussion).

The reward-associated distractor thus drew fast target-directed eye movements during saccadic flight, repulsed slow target-directed eye movements, made target-directed saccades generally slower and in some cases less accurate, and was more likely to capture the eyes to its location. This pattern is strikingly similar to that observed when the salience of the distractor is physically manipulated by increasing its luminance [7]. This is not a strategic effect: our participants knew to ignore objects at the distractor locations and that the colors of target and distractor were task irrelevant. There was no motivation or possibility for them to establish an attentional set for a specific color.

Reward — and its neurological correlate in the dopaminergic midbrain — is thought to motivate adaptive approach behaviour by driving humans and other animals to select, approach, and interact with objects similar to those that have garnered good outcome in the past [1]. The current results add to a growing literature suggesting that this type of reward-driven selection involves the action of low-level, non-strategic mechanisms that operate automatically [8–10]. Reward-associated stimuli draw our eyes, even when this is against our will.

### Supplemental Information

Supplemental Information includes two figures and supplemental experimental procedures and can be found with this article online at doi: 10.1016/j.cub.2012.02.007.

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[1]VU University Amsterdam, The Netherlands,
[2]Center for Mind/Brain Sciences (CIMeC), University of Trento, Italy.
E-mail: c.m.hickey@vu.nl, wieske.vanzoest@unitn.it