

Dynamic integration of information about salience and value for saccadic eye movements

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Humans shift their gaze to a new location several times per second. It is still unclear what determines where they look next. Fixation behavior is influenced by the low-level salience of the visual stimulus, such as luminance, contrast, and color, but also by high-level task demands and prior knowledge. Under natural conditions, different sources of information might conflict with each other and have to be combined. In our paradigm, we trade off visual salience against expected value. We show that both salience and value information influence the saccadic end point within an object, but with different time courses. The relative weights of salience and value are not constant but vary from eye movement to eye movement, depending critically on the availability of the value information at the time when the saccade is programmed. Short-latency saccades are determined mainly by salience, but value information is taken into account for long-latency saccades. We present a model that describes these data by dynamically weighting and integrating detailed topographic maps of visual salience and value. These results support the notion of independent neural pathways for the processing of visual information and value.

neuroeconomics | decision-making | cue combination | visual perception

Because of foveal specialization for high acuity and color vision, humans frequently move their eyes to project different parts of the visual scene on the fovea. Although the basic networks for the programming and execution of saccades have been studied for decades (1, 2), surprisingly little is known about the neural processes that underlie selection of the point of fixation of the next saccade. To some degree, the weighted combination of basic visual-stimulus features can predict saccadic eye movements in natural scenes (3–5). These basic stimulus features are, among others, local differences in luminance, color, or orientation and are combined by the visual system in a bottom-up image-based salience map. However, the salience difference between fixated and nonfixated image locations is typically rather small (6, 7), indicating that the influence of salience may be modulated by other factors. Visual salience, by definition, is determined by features of the visual scene alone and therefore is determined exclusively by visual bottom-up processing. Other factors reflect the influence of top-down processing. Task demands, for example, exhibit constraints on gaze patterns in different activities such as visual searching (8), manipulating an object (9), playing ball sports, preparing a cup of tea (10), and navigating between obstacles (11). In all these examples, gaze is concentrated on objects that are relevant for the task.

Along different lines, recent research in neuroeconomics has used saccadic eye movements as a tool to uncover the neural bases of primate choice behavior. The results of these experiments indicate that value can be an important determinant of the neural activity underlying the selection of a saccadic target when one object bears a higher reward than another (12–16). In these studies, a monkey observer typically selects between two or more spatially and visually distinct response alternatives that are associated with different rewards. Single-unit recordings have shown that the firing rates of some neurons in the lateral intraparietal

area (LIP) are indeed proportional to the relative expected subjective value. According to a “back-pocket” model of choice behavior (17), the LIP contains, in addition to a map of visual salience, a topographic map of value that is derived from dopaminergic cortical and striatal pathways. However, this research leaves open the question whether value is presented in the brain very coarsely for discriminating among a small number of different choices or is represented in full detail in a topographic map. We therefore devised a saccade task in which the expected gain varied smoothly as a function of saccadic end point, similar to tasks that have been used to study the effect of value on pointing behavior (18–20). Value has been shown to influence the fine-tuning of motor actions (e.g., pointing). In our saccade task, we also systematically manipulated the visual salience of our stimuli, because salience is known to be an important determinant of eye-movement behavior.

Results

We instructed our observers to make saccades from a central fixation point to a red stimulus patch composed of overlapping light and dark regions (Fig. 1*A*). We modulated the relative visual salience of the two regions by changing their relative contrast. In a salience baseline condition, observers were instructed simply to make a saccade to the red patch. No reward or penalty was given. We then varied value by changing the ratio of reward and penalty of either region (Fig. 1*B*). In the second condition, observers were informed that saccades to the darker region would be rewarded with 1.5 cents (as marked by the blue bars in Fig. 1*B*). In the third condition, observers were informed that, in addition to the rewards for saccades to the darker region, saccades to the lighter region would incur a 1.5-cent penalty (as marked by the orange bars in Fig. 1*B*). Observers were informed about the reward and penalty, but they were never explicitly instructed to saccade to a certain location within the stimulus patch. In Fig. 1, examples of the saccadic end-point distributions are shown for some conditions. In the baseline condition, in which a saccade did not incur a reward or a penalty, the relative contrast of the two regions exclusively determined the saccadic end points (Fig. 1*C* and *D*): When the contrast of the darker region was higher, saccadic end points shifted toward the darker region (Fig. 1*C*). When the contrast of the lighter region was higher, saccadic end points shifted toward the lighter region (Fig. 1*D*). However, when the region with lower contrast was rewarded and the region with higher contrast was penalized (Fig. 1*E*), the balance between light and dark was reversed, indicating that there is an inverse tradeoff between value and visual salience.

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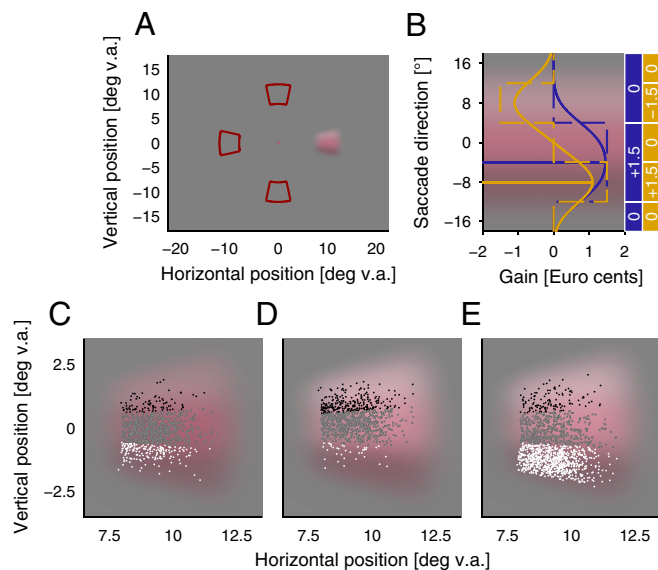


Fig. 1. Experimental paradigm and saccade end points of 10 observers. (A) Stimulus display. Observers initially fixated a bull's eye at (0,0), which disappeared 200 ms before the onset of the saccade target. The red lines indicate the three other possible target locations and were not part of the display. The relative position of the light and dark regions was randomized. (B) Gain landscape. The saccade score is shown for different directions of the saccade end points. The dashed lines show the given penalty and reward in the two value conditions. The solid lines represent the expected gain for the average variability across observers. The saccade direction yielding the maximum gain is marked by the solid horizontal lines. Blue and orange indicate the reward-only and the reward-and-penalty conditions respectively. (C–E), Saccade end points in the target for different conditions. End points in the dark region are plotted in white, end points in the light region are plotted in black, and intermediate end points are plotted in gray. All trials have been rotated and flipped, so that the target appears on the right side with the light region on top. Please note the difference between the saccade end points in C and D (salience effect) and between D and E (value effect). Trial conditions: C, contrast ratio of 20/10, no penalty or reward; D, contrast ratio of 20/40, no penalty or reward; E, contrast ratio of 20/40, reward and penalty.

Effects of Salience and Value. Because both salience and value information were manipulated only with respect to saccadic direction, we concentrate on this aspect of the data in the following quantitative analyses. We compared the distribution of observed saccadic directions and saccadic latencies with the predictions of a model that assumes an optimal selection of saccadic directions. The model is based on a dynamically weighted combination of salience and value, with inverse weights for salience and value (see below for model details). We hypothesized that visual salience-based saccades either always would be executed toward the region with the higher visual salience or would weight the relative visual salience of both regions in some manner. Fig. 2A shows average saccadic directions for conditions that differed only with respect to visual salience. In these conditions, saccadic latency had no effect on saccade direction [$F(5,45) = 1.09$, $P = 0.38$]; that is, differences in the low-level visual properties of the stimulus patch alone—its salience—fully accounted for the observed differences in the weighting of the two regions [$F(2,18) = 141.55$, $P < 0.001$].

In the conditions in which saccades to one of the regions were rewarded and saccades to the other region were penalized, the distribution of saccadic directions depended strongly on the value information and on the latency of the saccades. If value had no effect, one would expect the distribution of saccade directions to remain the same as in the salience-only condition. If the value alone determined the saccade direction, all saccades would land in the rewarded region. As shown in Fig. 2B and C,

visual salience alone could account for saccadic directions at the shortest latencies (<150 ms). The expected value determined saccadic directions at the longest latencies (>250 ms). At intermediate latencies, both sources of information were dynamically weighted, with the average saccade direction changing gradually from the more salient region to the rewarded region. This result indicates that the processing of value information is slower than saccade planning and that saccade planning proceeds without waiting for value information. The statistical analysis of saccadic directions showed significant main effects of value information [$F(2,18) = 79.20$, $P < 0.001$], visual salience [$F(2,18) = 65.46$, $P < 0.001$], and saccade latency [$F(5,45) = 50.08$, $P < 0.001$]. Furthermore, all pairwise interactions between these three variables were significant. Data of typical single observers are shown in Fig. S1.

Optimality Analysis. To estimate the dynamic weights of the processing of visual salience and value information, we compared the measured distributions of observed saccadic directions with the predictions of an optimality model. The model predicts optimal saccadic directions based on a dynamically weighted combination of salience and value at a given latency. To account for the effects of visual salience in the absence of reward or penalty, we averaged saccade directions separately for the different contrast conditions and used them as empirical estimates of visual salience. To account for differences in value, we calculated the saccadic direction that optimizes expected value, using a variant of the MEGaMove (Maximum Expected Gain) model. This model previously was applied successfully in similar experiments on manual pointing (18). For each possible saccade direction, the model calculates the expected value, based on the given parameters for penalty and reward and the variability of the individual observer's saccadic direction. This computation yields an expected value landscape that allows the selection of the saccade direction with the highest expected value. Depending on the relative ratio of the assigned rewards and penalties the optimal saccade direction shifts away from the penalized region toward the rewarded region (Fig. 1B). Note that for the reward-and-penalty condition the optimal saccade direction does not fall onto the center of the rewarded region but is shifted even further away from the penalized region. The measured distributions of saccadic directions followed the predictions of our model in the value conditions at long latencies (Fig. 2).

We modeled the transition from salience- to value-based saccades by a cumulative Gaussian function indicating the relative weight of visual salience and value (*SI Materials and Methods* and Fig. 3A). Using the same two parameters to fit both value conditions, our model produced an excellent fit of the observed saccade directions across all latencies (Fig. 3B and C). With only two free parameters, the model was able to explain on average $87 \pm 7\%$ of the variance of our data for the two value conditions. Estimated transition parameters were a mean of 184 ± 25 ms and a standard deviation of 32 ± 9 ms. These values indicate that saccades with latencies >184 ms were governed by value rather than by visual salience. The transition from 31% value to 69% value took 32 ms, on average. This transition also is reflected in the monetary gain. Saccades below the critical latency of 184 ms yielded an average gain of 0.3 cents per trial during the course of the whole experiment, whereas saccades above the critical latency yielded an average gain of 0.8 cents per trial. Depending on the condition, 30–60% of the saccades were above the critical latency (Fig. 3D).

Our results show that information about both visual salience and value is used to plan saccadic directions, that these two computations are performed independently, and that the neural computations for optimizing reward take significantly longer than the shortest latencies of saccades. This difference implies that a simple strategy to maximize expected value would be

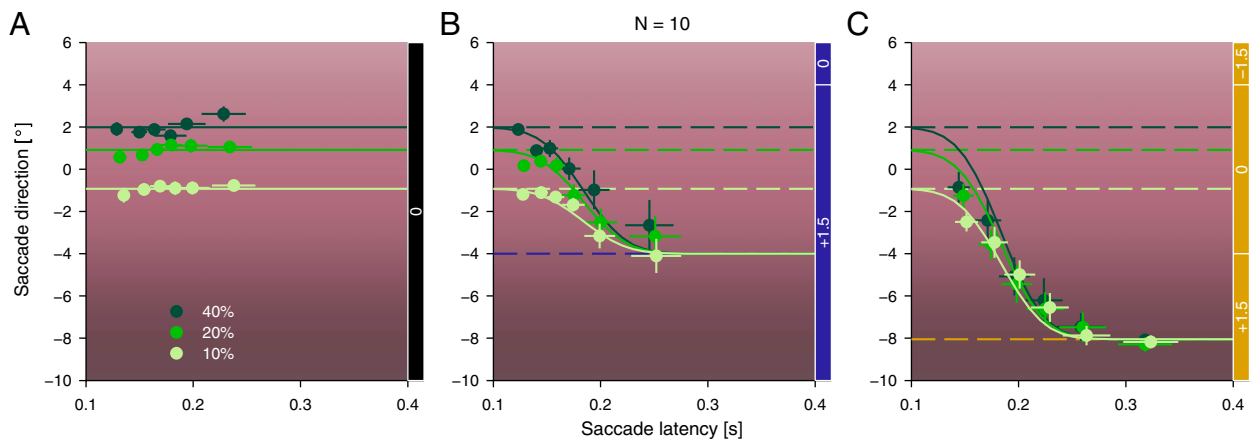


Fig. 2. Effect of visual salience and value information on saccade directions. Average saccade directions across 10 observers plotted over saccade latency. The different shades of green represent different contrast conditions. Green symbols and green solid lines represent the empirical data and the model fits, respectively. Saccade latencies are split into sextiles for each observer and each condition. Error bars represent the SEM across observers. The background shows the profile of the stimulus. The bars on the right side of the panels indicate the regions and values of reward and penalty. (A) Salience baseline condition. (B) Reward-only condition. (C) Reward-and-penalty condition. The blue (B) and orange (C) dashed lines mark the optimal saccade direction that maximizes gain based on the observer's individual saccadic variability and the reward:penalty ratio. The green dashed lines in B and C mark the predictions based on the salience baseline measurement in A.

always to wait to initiate eye movement until all value information is available. Our results show that our observers followed that strategy to some degree. The average saccade latencies were 177 ± 34 ms in the salience baseline condition, 174 ± 33 ms in the reward-only condition, and $221 \text{ ms} \pm 47$ ms in the reward-and-penalty condition [$F(2,18) = 4.85$, $P = 0.021$]. Indeed, it seems that our observers strategically increased their saccadic latencies depending on the speed of processing value information. The increase in latency was highly correlated with the time observers required to take value information into account ($r = 0.765$, $P = 0.01$). However, all observers still made many suboptimal saccades with short latencies in the conditions in which information about value had to be processed. There may be other possible constraints in the saccadic eye-movement system: There may be an inherent reward for fast saccades or an inherent penalty for slow saccades, or the built-in timing may be dominated by noise and thus cannot be controlled fully.

Effect of Learning. Another reason why observers make fast, suboptimal saccades may be that they must learn to delay their saccades. We therefore compared saccade latencies and saccade directions across successive trials as a function of trial number. Here we look only at the slowest 25% of saccades in the reward-and-penalty condition, because latencies are most variable in these data. During the course of the experiment, saccade latency increased from 236 ± 71 ms in the first 48 trials to 302 ± 81 ms in the last 48 trials [$F(22,198) = 2.14$, $P = 0.003$] (Fig. 4A). For the same subset of trials, saccade direction changed from $-5.1 \pm 3.0^\circ$ to $-8.2 \pm 1.5^\circ$ (Fig. 4B), further away from the penalty region [$F(22,198) = 1.60$, $P = 0.048$]. One of these observers needed more trials to learn to delay the saccades (Fig. S2). Two additional observers failed to delay their saccades and thus were unable to take value information into account (Fig. S3). Thus, observers are capable, at least partially, of delaying the latency of their saccades so that the saccadic system can take value information into account.

Corrective Saccades. Saccadic eye movements often land only in the vicinity of the intended target position. A secondary small saccade then is used to correct any remaining position error (21). In our experiment, observers executed a second saccade after the first saccade in $62 \pm 15\%$ of all trials. We therefore investigated whether salience and value drive these corrective saccades in the

same manner as the primary saccades. If the secondary saccades are influenced by value information, they should aim closer to the rewarded region than the primary saccades. Because the latencies of the secondary saccades were necessarily longer (414 ± 38 ms),

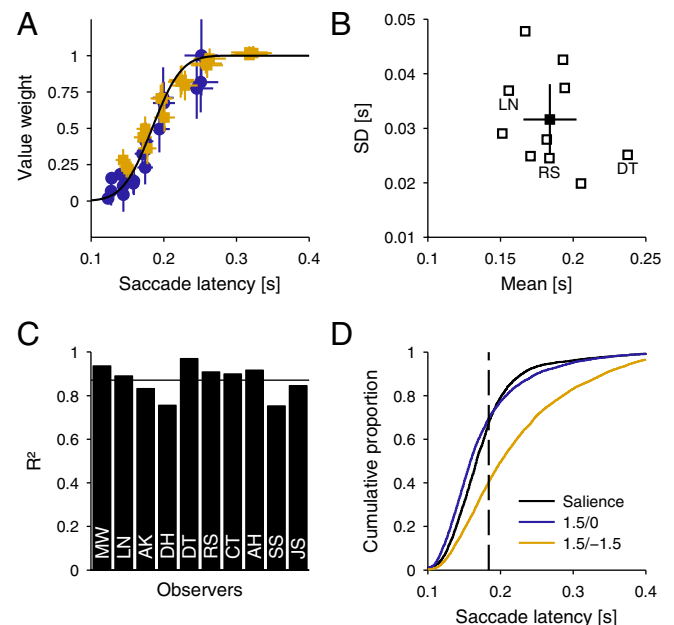


Fig. 3. Model of dynamic integration of visual salience and value. (A) Value weights. The symbols indicate the ratio of the observed and the optimal shift from salience to value. The line shows the fitted value weights estimated by the fits in Fig. 2 B and C. The blue circles and orange squares represent the reward-only and the reward-and-penalty conditions, respectively. Averaged data across 10 observers are shown. Error bars represent SEM. (B) Mean and SD of the cumulative Gaussian function fitted to estimate the relative weights of visual salience and value. Open squares show parameter estimates for the individual observers, and the filled square represents the mean across 10 observers. Error bars represent 95% confidence intervals. (C) R^2 of the model fits for 10 observers. The horizontal line represents the mean across observers. (D) Cumulative saccade latency for 10 observers. The dashed vertical line represents the mean of the cumulative Gaussian function, i.e., the latency at which the value weight reaches 0.5.

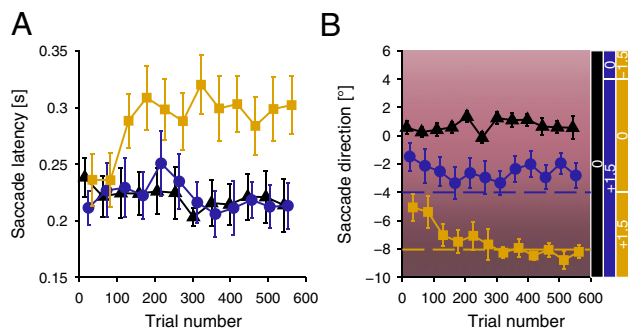


Fig. 4. Learning over trials. (A) Average saccade latency. (B) Average saccade direction. The blue and orange dashed lines mark the optimal saccade direction that maximizes gain based on the observer's individual saccadic variability and the given reward:penalty ratio. Black triangles show salience baseline condition, blue circles the reward-only condition, and orange squares the reward-and-penalty condition. Bin size is 48 trials. Error bars represent SEM.

our model indicates that value information should be readily available. The average time between the offset of the first saccade and the onset of the secondary saccade was 187 ± 26 ms, allowing the use of visual feedback when planning the secondary saccades. Indeed, the direction of the secondary saccades was influenced strongly by the value information [$F(2,18) = 127.05, P < 0.001$]. They landed close to the optimal directions predicted by our model (Fig. S4 A–C). Interestingly, more secondary saccades were executed in the reward-only ($74 \pm 15\%$) and the reward-and-penalty ($64 \pm 15\%$) conditions than in the salience baseline condition ($41 \pm 22\%$) [$F(2,18) = 19.96, P < 0.001$] (Fig. S4 D–F). Especially in the value conditions, more secondary saccades occurred for primary saccades with short latencies [$F(5,45) = 44.49, P < 0.001$]. The proportions of the secondary saccades and their measured directions suggest that they were driven by value information and served to correct the primary saccades. Once the value map is available, it is used automatically by the saccadic system, even though the secondary saccades themselves did not lead to rewards.

Saccade Trajectories. Assuming that information about value is integrated gradually into the planning of saccades, this process might be visible even in individual saccades. Although saccades are ballistic movements, the curvature of their trajectories is indicative of variables that affect early and late phases of planning (22). Because the gradual change from salience- to value-driven saccades was particularly pronounced in the reward-and-penalty condition, we concentrated on this condition for the analysis of saccade curvature. Here, even the average saccade trajectory was curved, and the curvature seemed to be more pronounced for saccades with longer latencies (Fig. S5A). For our analysis we computed the curvature for each saccade relative to a line connecting its start and end point. Saccade curvature depended critically on saccade latency [$F(5,45) = 16.97, P < 0.001$]: Saccades were straight or only slightly curved at short latencies but were strongly curved toward the rewarded region at long latencies (Fig. S5B). This curvature away from the penalized region is similar to the effects of visual distractors, which have been described as repelling saccades at long latencies (22).

Discussion

Our results show that both visual salience and value information determine saccadic end position but require different neural processing times. We compared the distribution of eye movements with the estimates of a model that predicts the saccadic end position based on a weighted combination of visual salience and value. Our

results demonstrate that visual salience dominates eye-movement planning for fast saccades, independently of the available rewards. Value information needs more time for processing and dominates the final eye position at longer latencies. The results indicate that a rich topographic representation of both salience and value is available to observers and that these two maps are combined additively within the visuomotor system.

Our results show that saccades share similar neural computations with other motor actions, in that value information can be used to control the final movement end point. Saccades differ from other movements in that the timing cannot be controlled fully to achieve optimal performance under all circumstances. Rather, value information seems to be integrated whenever it arrives in the brain regions responsible for the execution of saccades. Therefore, eye movements give us a unique opportunity to look at the dynamics of reward processing. Most other actions, such as pointing or grasping, have much longer latencies and movement durations. They exhibit close-to-optimal behavior in most cases (18, 20), because the reward computations have been performed fully by the time the movement starts.

Some of the brain regions that perform the neural computations underlying saccadic target selection have been identified already. The representation of a salience map has been associated with different brain areas; among them are areas in the early visual cortex V1 and V4 and oculomotor-related areas, such as the LIP area, the frontal eye fields (FEF), and the superior colliculi (SC) (23–27). The LIP area, FEF, and SC are of functional importance for eye movement planning and execution, as demonstrated by microstimulation in these areas (28–30). The LIP area and FEF have been shown to be influenced not only by bottom-up stimulus salience but also by top-down factors (13, 31), although value-based modulations might exist throughout the visual cortex (32). Recently it has been shown that the LIP area contains three signals (33–36): a bottom-up stimulus-onset signal, a saccade-related signal, and a cognitive, top-down signal that distinguishes targets from distractors. Interestingly, these different types of signals arrive at different latencies: The cognitive signal has latencies of about 117–133 ms, which is similar to our estimated delay for value processing (~ 184 ms), but the visual signal is much faster, at ~ 40 ms (33, 34). In summary, the LIP area likely contains a priority map that integrates bottom-up and top-down information to guide visuospatial attention and eye movements (37, 38). Top-down information about reward and loss likely is conveyed via the basal ganglia and the amygdala, respectively (39–41), and the combination of reward and loss signals presumably occurs in the prefrontal cortex (42, 43).

Even though the effects of reward have been investigated numerous times at the neural level, only a few studies have investigated the behavioral consequences of rewards for saccade planning and execution. These studies were concerned mostly with latencies of saccades, which are shortened for rewarded targets (44, 45). Interestingly saccade latencies do not reflect simply the magnitude or the probability of reward but rather the combination of magnitude and probability, i.e., the expected value (44). Reward also modulates saccade metrics such as the main sequence (46, 47), the relationship between the amplitude, the velocity, and the duration of a saccade (48). For example, saccades to neutral targets have a higher velocity and shorter duration when the subsequent presentation of a face is anticipated (47). Our findings on latencies agree with these earlier results and extend them by showing that the possibility of a loss can lead to longer latencies.

Our results also are relevant for the study of eye movements in visual search (see refs. 49 and 50 for reviews). In this paradigm, eye movements typically are not rewarded directly but can lead to a gain in information that subsequently might lead to a reward. There is some evidence that eye-movement strategies are explained best by computations based on maximizing the information gain (51–53). However, several studies show that at

least the first saccades in visual search are not optimal. First, the latency of the first saccade is not adjusted to the difficulty of the search task, resulting in a decrease in performance in more difficult tasks (54). Second, saccades do not always take into account the foveal and peripheral discriminability of potential targets in a search display (55). Third, the efficiency of saccadic decisions is well below the perceptual efficiency because saccades are programmed even before all available information has been integrated (56). Here we show that this lack of optimization holds not only for visual signals but even more for value information that takes longer to become available.

In general, the visuomotor system frequently seems to face the difficult task to integrate information that becomes available at different time scales. For example, when a stimulus is flashed briefly while the observer is executing smooth-pursuit eye movements, saccades can be directed either to its veridical spatial position or its retinal position at the time of the flash. To make a saccade to the veridical spatial position of the flash, information about the eye movements during the saccadic latency period must be taken into account. Interestingly, only saccades with latencies >175 ms are directed to the veridical spatial position (57). Similarly, information about retinal position and speed errors seem to arrive at different points in time. As a result, saccades become curved. The initial saccade trajectory is governed by the retinal position error and the late trajectory by retinal speed error (58). In all these cases, the need for a quick response must be balanced with the information that can be gained by delaying it. The linear combination of different cortical maps maybe an elegant way to perform this cortical computation.

Other recent studies have investigated directly the interaction between value and salience for saccadic target selection. Liston and Stone (59) performed an elegant experiment to investigate the effects of rewards on saccadic choices and brightness perception. They asked their observers to make a saccade to the brighter of two disks and then to compare the brightness of that disk with that of a third. They imposed a bias for leftward or rightward saccades by rewarding them. The rewards similarly biased saccadic and perceptual choices, indicating that any weighting of signals by rewards occurs before separate processing for perception and eye movements. It is an intriguing question whether the rewarded regions in our experiment might have appeared more saturated as well with the combined value and salience map being available for perception. Our paradigm does not allow an answer to the question, because effects of motor behavior or feedback connections are difficult to exclude with perceptual choices that take place at a much longer time scale. Because we were interested mainly in the dynamics and the topographic representation, we did not investigate any potential perceptual effects.

In the experiments reported by Navalpakkam et al. (60), observers had to saccade to one of eight possible targets that varied in salience and value. Neither value nor salience alone could account for the proportion of times a target was selected by the first saccade. The authors therefore proposed a Bayesian model that could account for the combination of these two variables. Unfortunately, saccadic latencies were not reported, so it is difficult to compare these results with ours. However, because the results for saccadic choices and for manual reactions were the same, it is likely that the results of these experiments depend mostly on the final state of the integration process. Markowitz et al. (16) did measure the time course of how value and salience information compete for visual selection. Monkey observers had to choose between two targets that were defined by congruent or incongruent salience and reward information. Matching our results, a dynamic and additive model fitted best. The switch from

salience- to value-dominated saccades occurred after 140–180 ms. These authors interpret their results in terms of exogenous and endogenous attention circuits (61) and assume that the effect of value on these decisions is mediated by attention, a point that has been raised before (62). The close relationship between attention and value is emphasized by recent results showing that neutral and task-irrelevant stimuli can capture attention if they previously have been associated with a reward (63). In general, it is difficult to dissociate attention and value in these experiments, and some authors even state that the purpose of attention is to maximize reward (64). Our results show that observers can shift their saccadic end points within a single object to maximize their reward; thus our results cannot be explained easily by spatial-, feature-, or object-based attention.

In conclusion, our results show that visual salience and value information are processed with different delays, resulting in a dynamic relative weighting of salience and value that depends on the timing of the saccade. This relative weighting likely reflects the ratio of neural activity in a priority map at the locations favored by salience and those favored by value. Saccades are programmed to the weighted average of these activation peaks, similar to averaging saccades to the center between two visual targets (65, 66). This programming implies the existence of a common map at some stage of visuomotor processing that includes information about salience, value, and perhaps other relevant signals. These topographic maps must be of high spatial resolution to be able to control the subtle changes in saccade position within a single object that we observed in our experiments. Interestingly, the dynamic integration of visual salience and value is visible only in saccadic eye movements, with their extremely fast latencies. Most other types of movements typically are executed at longer latencies, at which the processing of value information already is integrated completely in the corresponding priority maps.

Materials and Methods

Design. To test relative weights of visual salience and value information, we asked observers to saccade to a visual stimulus, a red patch containing two overlapping light and dark regions. To vary the relative visual salience, we varied the contrast of the light region. Each observer participated in three conditions. In the salience baseline condition, observers were instructed to make saccades to the patch without reward or penalty. The salience condition also contained single-stimulus conditions in which only one region was shown; we used this condition to measure the individual saccade variability of each observer. In the reward-only condition, observers were informed that they would win 1.5 cents for making saccades that ended in the dark region. In the reward-and-penalty condition observers were additionally instructed that they would lose 1.5 cents for making saccades that ended in the light region. In these two value conditions, observers received feedback about the end point of their saccades and the respective gain or loss resulting from their saccades. Specific details about observers, stimuli, equipment, and procedure are given in *SI Materials and Methods*.

Modeling. Our model uses a dynamic, weighted combination of salience and value to predict the observed distributions of saccade directions and latencies. We used the average saccade direction from the salience baseline condition as the salience-only prediction for the value conditions. The value-only prediction was the optimal saccade direction maximizing expected value. To compute this optimal direction, we used the given reward and penalty regions and the measured saccade variability from the single-stimulus condition, in which only one region was shown. The transition from salience-only to value-only predictions was estimated using a cumulative Gaussian function. Specific details about the model are given in *SI Materials and Methods*.

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