

# A unified selection signal for attention and reward in primary visual cortex

Liviu Stănişor<sup>a</sup>, Chris van der Togt<sup>a</sup>, Cyriel M. A. Pennartz<sup>b</sup>, and Pieter R. Roelfsema<sup>a,c,d,1</sup>

<sup>a</sup>Department of Vision and Cognition, Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts and Sciences, 1105 BA Amsterdam, The Netherlands; <sup>b</sup>Swammerdam Institute for Life Sciences, University of Amsterdam, 1098 SM Amsterdam, The Netherlands; <sup>c</sup>Department of Integrative Neurophysiology, Centre for Neurogenomics and Cognitive Research, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands; and <sup>d</sup>Psychiatry Department, Academic Medical Center, 1105 AZ Amsterdam, The Netherlands

Edited by Thomas D. Albright, The Salk Institute for Biological Studies, La Jolla, CA, and approved April 18, 2013 (received for review January 3, 2013)

**Stimuli associated with high rewards evoke stronger neuronal activity than stimuli associated with lower rewards in many brain regions. It is not well understood how these reward effects influence activity in sensory cortices that represent low-level stimulus features. Here, we investigated the effects of reward information in the primary visual cortex (area V1) of monkeys. We found that the reward value of a stimulus relative to the value of other stimuli is a good predictor of V1 activity. Relative value biases the competition between stimuli, just as has been shown for selective attention. The neuronal latency of this reward value effect in V1 was similar to the latency of attentional influences. Moreover, V1 neurons with a strong value effect also exhibited a strong attention effect, which implies that relative value and top-down attention engage overlapping, if not identical, neuronal selection mechanisms. Our findings demonstrate that the effects of reward value reach down to the earliest sensory processing levels of the cerebral cortex and imply that theories about the effects of reward coding and top-down attention on visual representations should be unified.**

object-based attention | reward expectancy

Reward and punishment shape behavior. The representations of actual and anticipated rewards in the brain are widespread and multifaceted (1–4). There are many brain areas that code the value, taste, and other perceptual qualities of incentive stimuli (5–14). Furthermore, rewards are motivating. Motivational effects influence neuronal activity in brain structures responsible for goal-directed behavior in cortex, in the basal ganglia, and also at the level of the superior colliculus where neurons increase their activity if larger rewards can be obtained (1, 3, 9, 15–19). Finally, rewards influence the choice of an animal (20, 21). If different stimuli are associated with distinct rewards, then it is optimal to choose the one with the highest expected value (22, 23). Neurons in the parietal and orbitofrontal cortex and also in the basal ganglia increase their activity for those stimuli that predict rewards that are larger or more probable (21, 22, 24–26).

Intriguingly, reward value also influences neuronal activity in early visual cortex. Shuler and Bear (27) demonstrated that neurons in rat primary visual cortex predict the timing of reward delivery, even in a phase of the task when the cells are not driven by a visual stimulus. This result is remarkable because primary visual cortex (V1) neurons are usually thought to code low-level visual features rather than stimulus value. Moreover, a functional magnetic resonance imaging (fMRI) study by Serences (28) demonstrated that reward value also influences V1 activity in humans. Subjects chose between two stimuli, and the one that was more rewarding evoked more activity. Apparently, the effects of reward value can reach back to the earliest cortical processing levels, where they might influence the coding of low-level features. However, the precise mechanisms responsible for these reward effects in early visual cortex, and in particular the relative importance of motivation and choice preference, have not yet been investigated.

Here, we studied the effects of reward value on neuronal activity in macaque V1. Moreover, we investigated the relationship between reward value and attention (29). The effects of attention are as

widespread across the brain as the effects of reward value (30, 31). It is remarkable that attention and reward value have usually been studied separately, because it is likely that their effects are related. Trials in which a high reward is at stake might cause a state of general attentiveness or arousal (19). Furthermore, reward value might influence “selective” attention; in the presence of multiple stimuli, attention might be attracted to those that are more rewarding. Studies on the neuronal correlates of expected value may therefore have measured attention shifts (29, 32). Conversely, selective attention studies instruct animals to attend one of a number of stimuli by rewarding behavioral responses to that stimulus and by not rewarding responses to distractors. Could there be a single selection signal in visual cortex that depends on value cues and attention cues?

Here, we compared the effects of reward and attention cues in area V1 with a curve-tracing task. We report that V1 activity depends on the value of a curve relative to the value of other curves. These relative value effects were abolished by an attentional cue. Relative value strongly influenced V1 activity by biasing the competition between curves, just like selective attention (33). Moreover, we found that the effects of relative value had a similar timing and magnitude as the effects of selective attention. Our results therefore suggest that reward and attention cues influence the same neuronal selection mechanism in visual cortex.

## Results

We trained monkeys in a curve-tracing task in which curves were associated with different rewards (Fig. 1A). The animals had to mentally trace a curve connected to a fixation point and to plan an eye movement to the end of this curve. In the first experiment (experiment 1), a trial began when the monkey directed gaze to a central fixation point and then two circular saccade targets and two curves appeared on the screen. Initially, the monkey did not know which curve had to be selected, but after 400 ms the target curve was cued by the appearance of an additional contour segment that made a connection between this curve and the fixation point (Fig. 1A, “connecting segment”). The monkey had to make an eye movement to the circle at the end of the target curve. The critical manipulation was that the saccade targets had three possible colors that were associated with different reward magnitudes. A red circle indicated high reward (0.2 mL of fruit juice), yellow indicated medium reward (0.1 mL), and green, no reward. There were nine combinations of colored circles (permutations of the colors of two circles), and we cued one of the two curves with the connecting segment so that there were 18 conditions in total. Saccades to the circle at the end of the distractor curve counted as errors. The monkeys learned to make

Author contributions: L.S., C.M.A.P., and P.R.R. designed research; L.S. performed research; L.S., C.v.d.T., and P.R.R. analyzed data; and L.S. and P.R.R. wrote the paper.

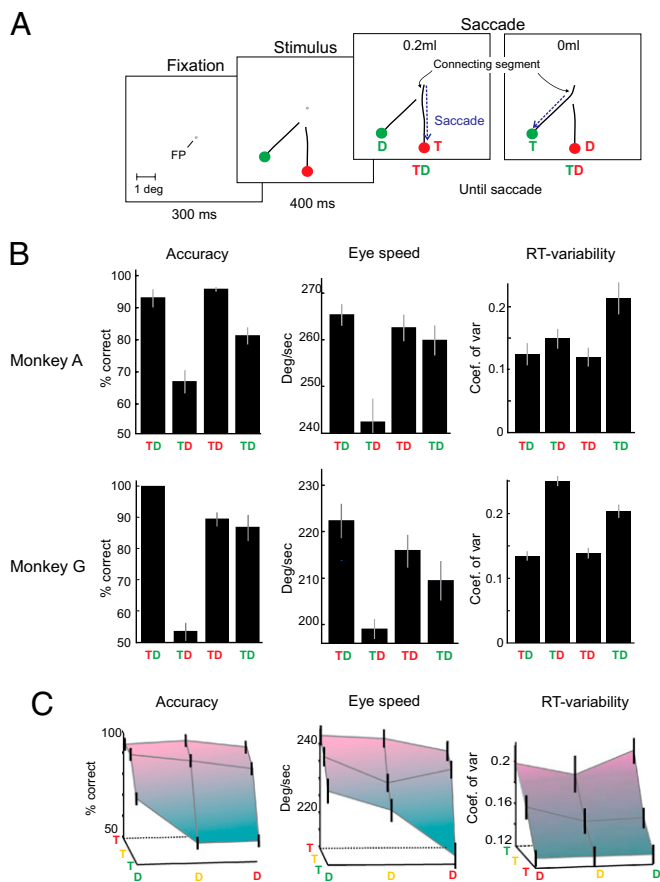
The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

<sup>1</sup>To whom correspondence should be addressed. E-mail: p.roelfsema@nin.knaw.nl.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1300117110/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1300117110/-DCSupplemental).



**Fig. 1.** Effects of reward value on behavior. (A) Curve-tracing task with varying rewards. The monkey directed gaze to a fixation point (FP) for 300 ms and then two curves appeared and two circles that were associated with different rewards (green, 0 mL; yellow, 0.1 mL; red, 0.2 mL of fruit juice). After 400 ms, a connecting segment appeared, cueing the monkey to make an eye movement (arrow) to the circle connected to the fixation point. (B) Accuracy (Left), eye speed (Middle), and variability in RT (Right) in the conditions with red and green circles (omitting conditions with yellow circles to avoid crowding). The colored letters denote reward magnitude associated with the target curve (T) and distractor curve (D). Red, high reward; green, no reward. Error bars denote SEM. (C) Behavioral measures averaged across animals for all reward cueing conditions. Note that the order of data points is different in the right panel to enhance visibility.

a saccade to the target circle even if it was green (no reward), because erroneous trials were repeated later in the block and a new block of trials started only after an accurate response to all stimuli. For convenience and in accordance with previous work, we will refer to the central connecting segment as an “attention cue” (34, 35) and to the colored circles at the end of the curves as “reward cues” (21, 36). The central question is whether these cues cause similar or distinct effects on V1 activity.

**Behavioral Analysis.** We first verified that the behavior of the monkeys was sensitive to the association between colors and rewards. A one-way ANOVA with the combination of colored circles as factor (nine color combinations) revealed a significant effect of the reward cues on the accuracy of both animals [Fig. 1 B and C; monkey A,  $F_{(8,45)} = 36.4, P < 10^{-3}$ ; monkey G,  $F_{(8,45)} = 98.8, P < 10^{-3}$ ]. Accuracy was higher if a high-reward target curve was combined with a no-reward distractor than for the opposite combination (monkey A, paired  $t$  test,  $P < 10^{-2}$ ; monkey G,  $P < 10^{-3}$ ). In accordance with previous studies (14, 18, 20, 37), eye movements had a higher speed if a high-reward target curve was accompanied by a no-reward

distractor than for the opposite combination (Fig. 1B) (both monkeys,  $t$  test,  $P < 10^{-3}$ ). Finally, reward cues influenced response times (RTs). One monkey produced shorter RTs to curves associated with higher reward, but the effects of reward on RT were less consistent in the other monkey (Fig. S1). However, there was a consistent effect on RT variability. The coefficient of variation of the RT was higher for the conditions with lower reward [Fig. 1 B and C; ANOVA, monkey A,  $F_{(8,45)} = 2.8, P < 0.02$ ; monkey G,  $F_{(8,45)} = 17.9, P < 10^{-3}$ ]. Thus, both animals were sensitive to the associations between colors and reward magnitudes.

**Effects of Reward Value on V1 Activity.** We next examined the influence of reward information on neuronal activity in V1 during the initial stimulus period when the monkeys did not yet know which eye movement would be required. We distinguished between two aspects of reward value (milliliters of juice): the “overall reward expectancy” and the “relative value.” For the definition of these quantities, we followed Milstein and Dorris (20) (see also ref. 21). The animal’s motivation is expected to depend on overall reward expectancy, i.e., the average of the two possible rewards while it is uncertain which curve will be cued:

$$\text{Expected\_reward} = \sum_j P(Cu_j) \cdot \text{reward}(Cu_j), \quad [1]$$

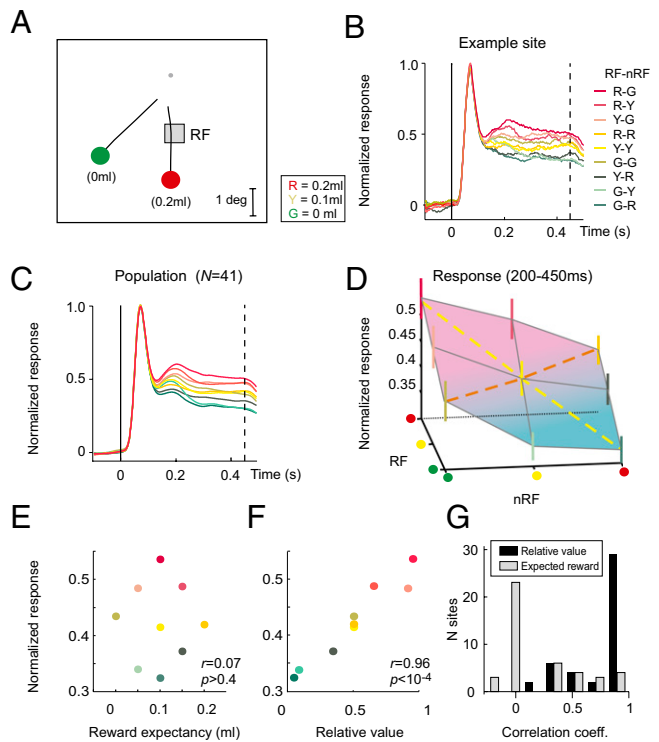
Here  $\text{reward}(Cu_j)$  is reward associated with curve  $j$  and  $P(Cu_j)$  is probability of cueing (50%). In contrast, choice preference should depend on the value of one curve relative to the other one. The relative value of a curve  $Cu_i$  is defined as follows:

$$\text{relative\_value}(Cu_i) = \frac{\text{reward}(Cu_i)}{\sum_j \text{reward}(Cu_j)}. \quad [2]$$

For example, if there is a curve with a red circle (0.2 mL) and one with a yellow circle (0.1 mL), the expected reward is 0.15 mL and the relative values are 0.67 and 0.33, respectively.

Fig. 2A shows the receptive field (RF) of an example V1 multiunit recording site. We always configured the stimulus so that the RF fell on a curve segment between the colored circle and the connecting segment, assuring that RF stimulation was identical on every trial. Fig. 2B illustrates how the neuronal response depended on the reward cues on correct trials. During the initial transient response, there was no influence of reward information, but during a later phase activity became strongest if the RF curve was associated with maximal reward and the other curve was associated with no reward (R-G), and weakest for the opposite color combination (G-R). The strength of the response was intermediate if the two curves were associated with equal rewards (G-G, Y-Y, and R-R). We used a one-way ANOVA (nine levels; all cue combinations) in window from 200 to 450 ms and found that the effect of the reward cues on response magnitude was highly significant [ $F_{(8,2713)} = 41.8; P < 10^{-6}$ ].

We observed similar effects across a population of 41 V1 recording sites (29 in monkey A and 12 in monkey G). A one-way ANOVA revealed a significant effect of the reward cues on activity [ $F_{(8,360)} = 11.3, P < 10^{-3}$ ] (Fig. 2 C and D). Neuronal activity was strongest if the RF curve was associated with a high reward and the other curve with no reward (R-G, red trace) and weakest for the opposite condition (G-R, green trace) (sign test,  $P < 10^{-10}$ ), which indicates that V1 activity depends on relative value (Fig. 2D, yellow dashed line). In contrast, the three stimuli where the amount of reward associated with the two curves was balanced evoked responses of similar strength, which indicates that the effect of overall reward expectancy was small (Fig. 2D, orange dashed line). Accordingly, the correlation between V1 response strength and overall reward expectancy was weak (Fig. 2E;  $r = 0.07; P > 0.4$ ), whereas relative value was a good predictor of V1 activity (Fig. 2F;



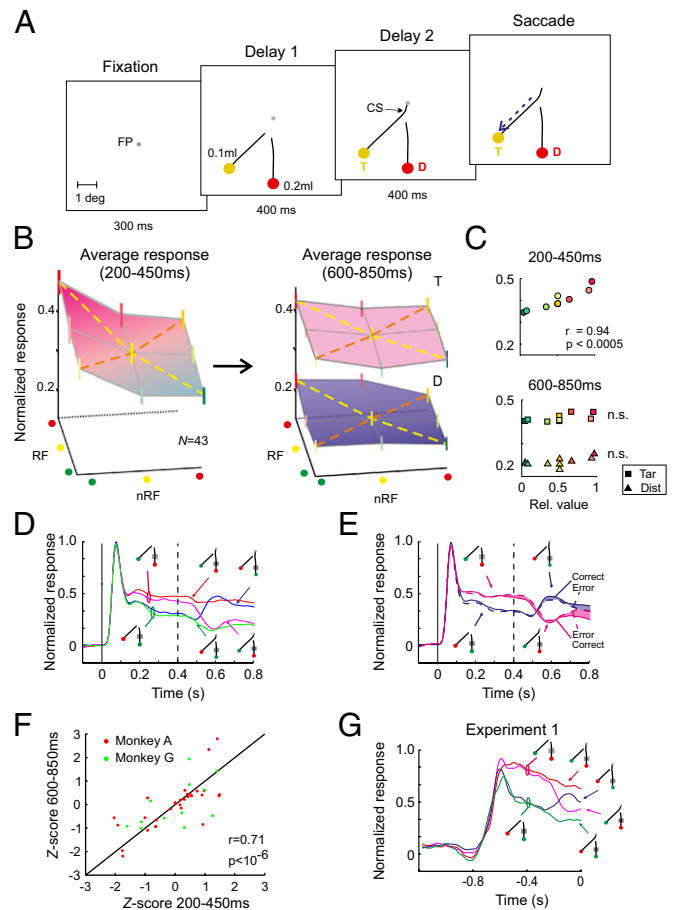
**Fig. 2.** Effect of reward information on neuronal activity in area V1. (A) Example stimulus and RF of one of the recording sites. (B) Neuronal activity evoked at the example recording site. The legend shows the combination of colors of the circles at the end of the curve in the RF and the other curve [not in the RF (nRF)]. (C) Activity averaged across the population of 41 recording sites in the two monkeys. (D) Average activity in a window from 200 to 450 ms after stimulus onset as function of the color of the circle at the end of the RF and nRF curve. Error bars represent SEM. The yellow dashed line connects conditions with varying relative value but constant overall reward expectancy (0.1 mL), whereas the orange line connects conditions with varying overall reward expectancy but constant relative value (0.5). (E and F) Neuronal activity as function of the overall reward expectancy (E) and relative value (F).  $r$  denotes correlation coefficient. (G) Correlation coefficients between neuronal activity at individual recording sites and overall reward expectancy (gray bars) and between neuronal activity and relative value (black bars).

$r = 0.96$ ;  $P < 10^{-4}$ ). Across individual recording sites, the average correlation coefficient between neuronal activity and relative value was 0.78 (median, 0.93), whereas the correlation with overall reward expectancy was 0.16 (median,  $-0.05$ ), significantly lower (Fig. 2G; paired  $t$  test,  $P < 10^{-6}$ ). Control analyses demonstrated that differences in eye position between conditions were not responsible for the effects of relative value (SI Text).

**Relationship Between Reward Value and Selective Attention.** Human observers solve the curve-tracing task by spreading visual attention over the target curve (38) and previous studies attributed the modulation of V1 activity to attention shifts (30). What is the relationship between the V1 response modulation caused by the central connecting segment (usually called central attention cue) and the new effect of relative value? In experiment 2, we used the same task, but introduced a second fixation delay of 400 ms so that we could also monitor V1 activity after cueing the target curve with the connecting segment (Fig. 3A). If reward cues and attention cues have separable effects, they are expected to interact in an additive manner and to influence independent groups of neurons. However, if there is a single neuronal selection mechanism at the level of V1, then (i) the neuronal effects of reward and attention cues might interact non-additively because the effect of one cue might occlude the effect of

the other one, and (ii) neurons influenced by reward cues should also be affected by the central attention cues.

During the first delay (200–450 ms), relative value was a good predictor of V1 activity just as in experiment 1 [ANOVA,  $F_{(8,378)} = 99$ ,  $P < 10^{-6}$ ] (Fig. 3B, Left), and the correlation coefficient was 0.94 (Fig. 3C, Upper). Once the connecting segment appeared, however, the response evoked by the target curve became stronger than the response evoked by the distractor curve, whereas the colored circles lost their influence (Fig. 3B, Right). A two-way ANOVA with factors reward condition and target/distractor during the second delay (600–850 ms) revealed a significant effect of target/distractor [ $F_{(1,756)} = 395$ ,  $P < 0.001$ ] but no effect of reward cues [ $F_{(8,756)} = 1.5$ ,  $P > 0.1$ ].



**Fig. 3.** Comparison of reward and attention modulation. (A) The monkey had to maintain fixation for 400 ms after the appearance of the connecting segment (CS). The disappearance of the fixation point cued the monkey to make a saccade. (B) Neuronal activity as function of the color of the two curves. Left shows neuronal activity in the first delay, and Right, activity in the second delay. Error bars represent SEM. (C) Correlation between relative value and V1 activity during the first epoch (Upper) and the second epoch evoked by the target (squares) and distractor curve (triangles). The correlations in the second epoch were nonsignificant (n.s.). (D) The average activity in the conditions with maximal and minimal relative value. Insets denote conditions and position of RF (gray square). (E) Error trials. Magenta curves show activity evoked by the noncued high-reward curve on correct (continuous line) and error trials (dashed line) and blue curves activity evoked by the cued no-reward curve. (F) Correlation between the Z scores of the attention (ordinate,  $MI_{Att}$ ) and reward modulation index (abscissa,  $MI_{Rew}$ ). Red data points are from monkey A ( $n = 29$ ), and green data points from monkey G ( $n = 12$ ). (G) Effect of the central attention cues in experiment 1. Neuronal activity is aligned on the onset of the saccade (time 0). V1 neurons select the target curve before the saccade even if the RF falls on the no-reward curve (blue curve) and deselect the high-reward distractor (magenta).

In this epoch, the correlation between V1 activity and relative value became nonsignificant (Fig. 3C, *Lower*). Fig. 3D illustrates the population response for conditions where the RF curve had a maximal or minimal relative value. Activity evoked by a curve with a high relative value stayed high if it became target (Fig. 3D, red trace), but decreased if it became a distractor (magenta). Conversely, activity evoked by a curve with a low relative value stayed low if it became distractor (green), but increased to the level evoked by a high reward curve if it became target (blue). Thus, effects of the central cue (the connecting segment) replaced the reward cuing effects during the second delay if the monkey accurately selected the target curve.

In error trials, the central cue did not replace the reward cuing effect. We focused our error analysis on trials with a high-reward and a no-reward curve. As expected, the monkeys made more errors when the no-reward curve was cued as target (29% errors) than when the high-reward curve was cued (3%). We compared V1 activity on error trials to that on correct trials. As mentioned above, the V1 response evoked by the no-reward target curve increased to the level of a high-reward target curve on correct trials (Fig. 3E, blue continuous curve), but on error trials the activity increase was weaker [blue dashed trace;  $t_{(42)} = 3.7$ ,  $P < 0.001$ , window from 600 to 850 ms]. Conversely, the V1 activity evoked by the high-reward distractor curve decreased after presentation of the central cue (Fig. 3E, magenta continuous trace), but the activity decrease was less pronounced if the monkey erroneously selected the distractor [magenta dashed trace;  $t_{(42)} = 8.0$ ,  $P < 10^{-6}$ ]. Thus, the central cue only abolished the reward cuing effects in V1 on correct trials. This overriding effect predicted accurate performance.

To investigate whether the effects of the reward cues and the central attention cues are correlated across neurons, we calculated a reward modulation index ( $MI_{\text{rew}}$ ) in the first delay using conditions with the most extreme relative values,  $MI_{\text{rew}} = (R_{\text{High}} - R_{\text{No}}) / (R_{\text{High}} + R_{\text{No}})$ , and compared it to an attentional modulation index,  $MI_{\text{Att}} = (R_{\text{T}} - T_{\text{D}}) / (R_{\text{T}} + R_{\text{D}})$ , during the second delay. We found a significant correlation between  $MI_{\text{rew}}$  and  $MI_{\text{Att}}$  across sites in monkeys A [ $r = 0.75$ ,  $t_{(29)} = 6.1$ ,  $P < 10^{-6}$ ] and G [ $r = 0.59$ ,  $t_{(10)} = 2.3$ ,  $P < 0.025$ ]. When we pooled data across the two monkeys after normalizing the range of MIs per monkey by computing Z scores, the correlation coefficient was 0.71 [ $t_{(41)} = 6.4$ ,  $P < 10^{-6}$ ] (Fig. 3F). This strong correlation indicates that reward cues and central attention cues drive the same selection process in V1.

The second epoch of experiment 2 facilitated the analysis of the interaction between cues. However, we observed the same interaction in the short period between the appearance of the central cue and the saccade in experiment 1 if we aligned neuronal activity to saccade onset. If the V1 RF fell on the high reward curve in experiment 1, activity was high (Fig. 3G, red trace) and stayed high if this curve was cued as target but decreased if it became a distractor [magenta; 0- to 200-ms window before the saccade,  $t_{(43)} = 11.6$ ,  $P < 10^{-6}$ ]. Conversely, V1 activity was low before the appearance of the central cue if the RF fell on the no-reward curve and stayed low if this curve became distractor (green trace) but increased if it became target [blue;  $t_{(43)} = 9.1$ ,  $P < 10^{-6}$ ], in accordance with the conjoint influence of the reward and attention cues on V1 activity.

To further investigate the relationship between the effect of reward cues and central attention cues, we determined the latency of their effects (Fig. S2). The latency of reward modulation was 118 ms and it did not differ significantly from the effect of the central cues with a latency of 119 ms. Thus, the effects of these two types of cues also have a similar timing.

### Reward Modulation Is Strongest in the Presence of Multiple Curves.

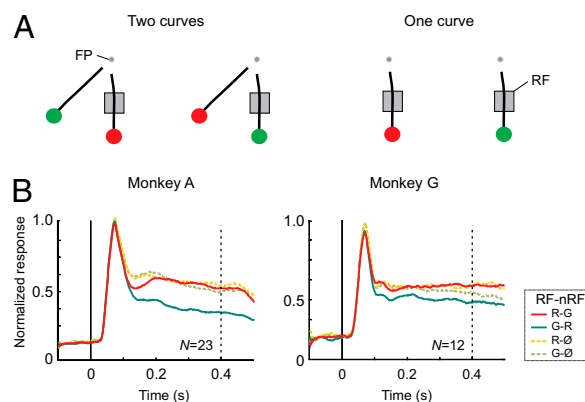
Relative value and central attention cues cause a similar modulation of V1 activity. Selective attention effects are most pronounced in the presence of competing stimuli (33), and we tested whether this also holds true for the new reward cuing effect. In experiment 3, we presented either two curves where one curve was associated with a high reward and the other with no reward, or a single curve

associated with high or no reward (Fig. 4A). As in our previous experiments, we observed strong effects of relative value in the two-curve condition (Fig. 4B). In the presence of a single curve, however, the effect of the reward cues was smaller and the activity was close to that evoked by the high-reward curve of the two-curve condition. In the two-curve condition, the average  $MI_{\text{rew}}$  was 0.23, which was significantly larger than the value of 0.05 in the one-curve condition (paired  $t$  test,  $P < 10^{-6}$  for both monkeys). The  $MI_{\text{rew}}$  in the one curve condition was nevertheless significantly larger than zero (sign test,  $P < 10^{-5}$  for monkey A and  $P < 0.05$  for monkey G). Thus, we observed a small but significant effect of reward information with a single curve and a fourfold to fivefold stronger effect with two curves. Thus, the effects of the reward cues on V1 activity are most pronounced in the presence of competing stimuli.

### Discussion

We found that the relative value of a stimulus influences V1 activity. Our results imply a comparison process that evaluates the value of the colors at the end of the curves, increasing activity at the circle with the higher value. We always placed the neurons' RFs on the curve but not on the circle itself, and the increased neuronal activity must therefore have spread from the circle onto the curve, suggesting that reward information influences neuronal activity in an object-based manner. Effects of reward value have been reported previously for rat area V1 (27) and also in human visual cortex with fMRI (28, 39, 40). The findings of this study are compatible with these previous results, but they also go beyond by showing that reward effects in V1 are mostly driven by relative value, which is a quantity that is useful for the guidance of choice behavior. At the same time, we found that the effect of motivation as indexed by overall reward expectancy was relatively weak. Comparable effects have previously been observed in the lateral intraparietal area (area LIP) (21, 24, 36, 41) and in premotor cortex (42), where the relative value of a stimulus has a strong effect but overall reward expectancy does not. The widespread influence of relative value on neuronal activity in brain regions as diverse as the premotor and primary visual cortex underlines the importance of this signal (22, 43), and the present results establish that relative value is coded in an object-based manner.

The relationship between the effects of reward value and attention cues on neuronal activity in the visual cortex has remained unclear in previous work. In an influential study on the coding of decision variables, Platt and Glimcher (21) argued that neurons in area LIP of parietal cortex coded the value of stimuli. This view was

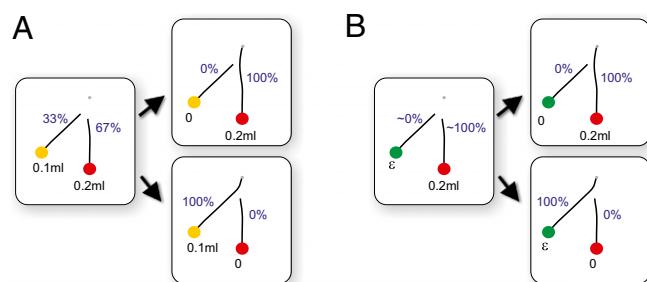


**Fig. 4.** Effect of reward information for stimuli with one and two curves on activity in V1. (A) The monkeys saw two curves associated with different rewards (*Left*) or a single curve (*Right*). The colored circle at the end of each curve signaled high reward (0.2 mL, red) or no reward (green). FP, fixation point; RF, receptive field. (B) Population response evoked by the high- and no-reward curve in the presence of a second curve (red and green traces) and if presented alone (yellow and green dashed traces).

later challenged (29, 32) because the reward effect had not been dissociated from attention shifts. Here, we used an experimental design similar to that of Platt and Glimcher (21) in V1, an area not thought to have a specific role in the coding of decision variables but known to be modulated by attention shifts (30, 44). The present results show that the effects of the reward cues on neuronal activity in V1 are the same as the effects of central attention cues in many respects. First, the modulation of V1 activity by reward and attention cues has a similar latency of  $\sim 120$  ms (45). Second, the modulation by reward value is strongest in the presence of competing stimuli, just as has been observed for selective attention (33). Third, the strength of the response modulation caused by reward cues predicts the effect of attention cues across recording sites. Our multiunit recording technique did not permit us to investigate this correlation at the level of single units, but clusters of neurons with a strong effect of reward cues also expressed a strong effect of attention cues. Fourth, reward cues had little effect after the appearance of the central attention cue if the monkey correctly selected the target curve, which implies a nonadditive, unitary effect of the two types of cues. However, there was a residual effect of the reward cues on V1 activity in erroneous trials, which implies that the central cues had to reverse the unitary selection signal for accurate performance.

Why do reward-predicting cues and central attention cues cause similar effects in V1? A likely explanation is that the central cues also influence the relative value of the two curves. An eye movement to the distractor was never rewarded and the relative value of the target curve therefore always became 100% after the appearance of a central cue, whereas the relative value of the distractor became zero (Fig. 5A). The finding that the central cues supersede the colored reward cues is therefore in accordance with an effect of relative value. We found that a target curve associated with no reward evoked a V1 response that was comparable to that evoked by a high-reward target curve. This high level of activity can also be explained as an effect of relative value, because the monkeys had to select the zero-reward target curve to gain access to later trials with larger rewards. Thus, if rewards in the more remote future are taken into account (46), the value of a zero-reward target curve is small but positive ( $\epsilon$  in Fig. 5B; see *SI Text* for additional details), whereas the value of a distractor is zero, so that the relative value of the target curve becomes 100%. Relative value can also explain the comparatively small effect of reward value on V1 activity if there is only a single curve, which by the same reasoning always has a relative value of 100%. Thus, across our experiments, the level of V1 activity in the delayed response phase was well predicted by relative value.

The present results support the hypothesis that studies on selective attention (33, 34, 47, 48) and relative value (21, 24, 28, 41, 47)



**Fig. 5.** The effect of the connecting segment on relative value. (A) The connecting segment focuses reward on the target curve so that the relative value of this curve increases to 100%. Black numbers show the amount of reward associated with individual curves. Blue numbers denote relative value. (B) A correct saccade to the green circle at the end of a target curve is inferred to yield a small, indirect reward  $\epsilon$  because it gives access to future trials in which real rewards can be gained. Therefore, the relative value of a target curve with a green circle equals 100% (Bottom).

in the visual cortex investigated the same selection process. Researchers usually train monkeys to process “attentional” cues by varying reward contingencies, e.g., by only rewarding the monkey for responses to one (attended) stimulus and by not rewarding for responses to another (ignored) stimulus. Vice versa, it is likely that studies on reward processing influence the distribution of selective attention across the stimuli in a display. If our interpretation of a single selection process is correct, then the present results show that the attentional enhancement of neuronal responses in visual cortex is proportional to the relative value of stimuli (Fig. 2F). In other words, rewarding stimuli attract attention in proportion to their value. Thus, the visual cortex highlights stimuli with a high relative value (47), and the same holds true for stimuli that need to be processed to gain access to rewards (see, e.g., ref. 48).

The computation of relative value requires a comparison between stimuli that can be far apart in the visual field and it is therefore likely that the modulation of V1 activity depends on feedback from higher visual and frontal areas and the amygdala where the representation of reward value depends less on the spatial configuration of stimuli (7, 8, 49). Feedback from these higher brain regions to visual cortex could explain why the relative value effects are expressed during a delayed phase of the neuronal response. Future studies could determine the source of the V1 selection signals in brain regions that store the associations between visual stimuli and rewards.

## Materials and Methods

We recorded neuronal activity from area V1 of two head-fixed monkeys with chronically implanted electrode arrays. Our procedures complied with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals* (50) and were approved by the Institutional Animal Care and Use Committee of the Royal Netherlands Academy of Arts and Sciences. In a first operation, a head holder was implanted and a gold ring was inserted under the conjunctiva of one eye for the measurement of eye position. In a separate operation, arrays of  $4 \times 5$  or  $5 \times 5$  electrodes (Blackrock) with an impedance of 0.1–0.8 M $\Omega$  (at 1 kHz) and a thickness of 80  $\mu$ m were implanted chronically in V1. The surgical procedures were performed under aseptic conditions and general anesthesia. Details of the surgical procedures and the postoperative care have been described elsewhere (34).

**Behavioral Tasks.** The animals performed a curve-tracing task in which they had to locate a circular target that was connected to the fixation point by a curve (target curve) and to ignore a distracting curve not connected to the fixation point (Fig. 1A). A trial started as soon as the monkey’s eye position was within a  $1.2^\circ \times 1.2^\circ$  window centered on a fixation point. After an interval of 300 ms, the stimulus appeared on the screen. Both curves were initially not connected to the fixation point and had circular targets at their ends with a varying color. The color of the circle signified the amount of reward that the monkey would receive if cued to make an eye movement to it. Red, yellow, and green signaled a high amount (0.2 mL), an intermediate amount (0.1 mL), and no fruit juice, respectively. The monkeys had to maintain fixation for 400 ms, and then a connecting segment appeared that attached the target curve to the fixation point. In experiments 1 and 3, the appearance of the connecting segment was the cue to make an eye movement to the circle at the end of the target curve. In experiment 2, the monkey had to maintain fixation for another 400 ms after the appearance of the connecting segment. In experiments 1 and 2, there were a total of 18 conditions because we crossed the nine possible combinations of two colored circles with two connecting segments. In experiment 3, there were six conditions. Four of these had two curves, one of which was associated with a high reward and the other with no reward (two stimuli) crossed with cueing of the high-reward or no-reward curve (two cueing conditions). The other two conditions had a single curve associated with high or no reward that was always cued. In all experiments, the stimuli were randomly interleaved and occurred in blocks of trials. The monkey had to give a correct response to every stimulus of the block before a new block started. We recorded at least 50 correct trials per stimulus for every recording site. For the analysis of behavior (Fig. 1), we used data from six sessions in each monkey and we focused our analysis on trials where the monkeys made a saccade to either circle so that an accuracy of, e.g., 70% means that the monkey made a saccade to the wrong circle on 30% of the trials.

**Recording of Multiunit Activity and Data Analysis.** Spiking activity was recorded from the chronically implanted multielectrode arrays with Tucker-Davis Technologies (TDT) recording equipment. We recorded from the same recording sites across days, which permitted us to obtain reliable data despite a relatively large number of conditions (e.g., 18 conditions in experiment 2). For every recording site, we first normalized the activity to the peak response per session (*SI Text*) and then averaged across sessions. Every recording site therefore contributed a single data point to the statistics. Further details

about the recording method, the RF properties, the measurement of latency, and the definition of relative value and modulation index have been specified in *SI Text*.

**ACKNOWLEDGMENTS.** We thank Kor Brandsma and Dave Vleesenbeek for technical support. The work was supported by an Netherlands Organization for Scientific Research (NWO)-VICI grant, a grant of the NWO Excellence Program Brain and Cognition, and a Human Frontier Science Program grant.

- Leon MI, Shadlen MN (1999) Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron* 24(2):415–425.
- Schultz W (2007) Multiple dopamine functions at different time courses. *Annu Rev Neurosci* 30:259–288.
- Hikosaka O, Nakamura K, Nakahara H (2006) Basal ganglia orient eyes to reward. *J Neurophysiol* 95(2):567–584.
- Rangel A, Camerer C, Montague PR (2008) A framework for studying the neurobiology of value-based decision making. *Nat Rev Neurosci* 9(7):545–556.
- Watanabe M (1996) Reward expectancy in primate prefrontal neurons. *Nature* 382(6592):629–632.
- Tremblay L, Schultz W (1999) Relative reward preference in primate orbitofrontal cortex. *Nature* 398(6729):704–708.
- Padoa-Schioppa C, Assad JA (2006) Neurons in the orbitofrontal cortex encode economic value. *Nature* 441(7090):223–226.
- Paton JJ, Belova MA, Morrison SE, Salzman CD (2006) The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature* 439(7078):865–870.
- Lauwereyns J, Watanabe K, Coe B, Hikosaka O (2002) A neural correlate of response bias in monkey caudate nucleus. *Nature* 418(6896):413–417.
- Lansink CS, et al. (2008) Preferential reactivation of motivationally relevant information in the ventral striatum. *J Neurosci* 28(25):6372–6382.
- Schultz W, Dickinson A (2000) Neuronal coding of prediction errors. *Annu Rev Neurosci* 23:473–500.
- Rudebeck PH, et al. (2008) Frontal cortex subregions play distinct roles in choices between actions and stimuli. *J Neurosci* 28(51):13775–13785.
- Thorpe SJ, Rolls ET, Maddison S (1983) The orbitofrontal cortex: Neuronal activity in the behaving monkey. *Exp Brain Res* 49(1):93–115.
- Kobayashi S, et al. (2006) Influences of rewarding and aversive outcomes on activity in macaque lateral prefrontal cortex. *Neuron* 51(6):861–870.
- Ikeda T, Hikosaka O (2003) Reward-dependent gain and bias of visual responses in primate superior colliculus. *Neuron* 39(4):693–700.
- Morrison SE, Salzman CD (2009) The convergence of information about rewarding and aversive stimuli in single neurons. *J Neurosci* 29(37):11471–11483.
- Roesch MR, Olson CR (2004) Neuronal activity related to reward value and motivation in primate frontal cortex. *Science* 304(5668):307–310.
- Kawagoe R, Takikawa Y, Hikosaka O (1998) Expectation of reward modulates cognitive signals in the basal ganglia. *Nat Neurosci* 1(5):411–416.
- Roesch MR, Olson CR (2007) Neuronal activity related to anticipated reward in frontal cortex: Does it represent value or reflect motivation? *Ann N Y Acad Sci* 1121:431–446.
- Milstein DM, Dorris MC (2007) The influence of expected value on saccadic preparation. *J Neurosci* 27(18):4810–4818.
- Platt ML, Glimcher PW (1999) Neural correlates of decision variables in parietal cortex. *Nature* 400(6741):233–238.
- Glimcher PW (2003) The neurobiology of visual-saccadic decision making. *Annu Rev Neurosci* 26:133–179.
- Gold JI, Shadlen MN (2007) The neural basis of decision making. *Annu Rev Neurosci* 30:535–574.
- Sugrue LP, Corrado GS, Newsome WT (2004) Matching behavior and the representation of value in the parietal cortex. *Science* 304(5678):1782–1787.
- Lau B, Glimcher PW (2008) Value representations in the primate striatum during matching behavior. *Neuron* 58(3):451–463.
- van Duuren E, et al. (2009) Single-cell and population coding of expected reward probability in the orbitofrontal cortex of the rat. *J Neurosci* 29(28):8965–8976.
- Shuler MG, Bear MF (2006) Reward timing in the primary visual cortex. *Science* 311(5767):1606–1609.
- Serences JT (2008) Value-based modulations in human visual cortex. *Neuron* 60(6):1169–1181.
- Maunsell JHR (2004) Neuronal representations of cognitive state: Reward or attention? *Trends Cogn Sci* 8(6):261–265.
- Roelfsema PR (2006) Cortical algorithms for perceptual grouping. *Annu Rev Neurosci* 29:203–227.
- Schall JD, Thompson KG (1999) Neural selection and control of visually guided eye movements. *Annu Rev Neurosci* 22:241–259.
- Leathers ML, Olson CR (2012) In monkeys making value-based decisions, LIP neurons encode cue saliency and not action value. *Science* 338(6103):132–135.
- Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 18:193–222.
- Roelfsema PR, Lamme VAF, Spekreijse H (1998) Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 395(6700):376–381.
- Roberts M, Delicato LS, Herrero J, Gieselmann MA, Thiele A (2007) Attention alters spatial integration in macaque V1 in an eccentricity-dependent manner. *Nat Neurosci* 10(11):1483–1491.
- Louie K, Gratton LE, Glimcher PW (2011) Reward value-based gain control: Divisive normalization in parietal cortex. *J Neurosci* 31(29):10627–10639.
- Takikawa Y, Kawagoe R, Itoh H, Nakahara H, Hikosaka O (2002) Modulation of saccadic eye movements by predicted reward outcome. *Exp Brain Res* 142(2):284–291.
- Houtkamp R, Spekreijse H, Roelfsema PR (2003) A gradual spread of attention during mental curve tracing. *Percept Psychophys* 65(7):1136–1144.
- Serences JT, Saproo S (2010) Population response profiles in early visual cortex are biased in favor of more valuable stimuli. *J Neurophysiol* 104(1):76–87.
- Armony JL, Dolan RJ (2002) Modulation of spatial attention by fear-conditioned stimuli: An event-related fMRI study. *Neuropsychologia* 40(7):817–826.
- Dorris MC, Glimcher PW (2004) Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* 44(2):365–378.
- Pastor-Bernier A, Cisek P (2011) Neural correlates of biased competition in premotor cortex. *J Neurosci* 31(19):7083–7088.
- Cisek P, Kalaska JF (2010) Neural mechanisms for interacting with a world full of action choices. *Annu Rev Neurosci* 33:269–298.
- Poort J, Roelfsema PR (2009) Noise correlations have little influence on the coding of selective attention in area V1. *Cereb Cortex* 19(3):543–553.
- Roelfsema PR, Khayat PS, Spekreijse H (2003) Subtask sequencing in the primary visual cortex. *Proc Natl Acad Sci USA* 100(9):5467–5472.
- Nakahara H, Itoh H, Kawagoe R, Takikawa Y, Hikosaka O (2004) Dopamine neurons can represent context-dependent prediction error. *Neuron* 41(2):269–280.
- Peck CJ, Jangraw DC, Suzuki M, Efem R, Gottlieb J (2009) Reward modulates attention independently of action value in posterior parietal cortex. *J Neurosci* 29(36):11182–11191.
- Treue S, Maunsell JHR (1996) Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382(6591):539–541.
- Matsumoto K, Suzuki W, Tanaka K (2003) Neuronal correlates of goal-based motor selection in the prefrontal cortex. *Science* 301(5630):229–232.
- National Research Council, Committee for the Update of the Guide for the Care and Use of Laboratory Animals, and Institute for Laboratory Animal Research (2011) *Guide for the Care and Use of Laboratory Animals* (National Academies Press, Washington, DC), 8th Ed.