Overlapping circuits for relative value and selective attention in primary visual cortex

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ABSTRACT

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 demonstrate that the reward value of a stimulus relative to the value of other stimuli is a good predictor of activity in the primary visual cortex (area V1). Relative value biases the competition between stimuli and this effect of reward resembles the effect of attentional selection in its latency and strength across the V1 neuronal population. These findings demonstrate that the effects of reward value and selective attention are interdependent at the earliest levels of sensory processing in the cerebral cortex and they therefore inspire a unification of theories of reward coding and top-down attention.

INTRODUCTION

Reward and punishment shape behavior. The representations of actual and anticipated reward in the brain are therefore widespread and multifaceted (Hikosaka et al., 2006; Leon and Shadlen, 1999; Rangel et al., 2008; Schultz, 2007). There are many brain areas that code the value, taste and other perceptual qualities of incentive stimuli (Kobayashi et al., 2006; Lansink et al., 2008; Lauwereyns et al., 2002; Padoa-Schioppa and Assad, 2006; Paton et al., 2006; Rudebeck et al., 2008; Schultz and Dickinson, 2000; Thorpe et al., 1983; Tremblay and Schultz, 1999; Watanabe, 1996). 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 (Hikosaka et al., 2006; Ikeda and Hikosaka, 2003; Kawagoe et al., 1998a; Lauwereyns et al., 2002; Leon and Shadlen, 1999; Morrison and Salzman, 2009; Roesch and Olson, 2004; Roesch and Olson, 2007). Finally, rewards influence the choice of an animal (Milstein and Dorris, 2007; Platt and Glimcher, 1999). If different stimuli are associated with distinct rewards then it is optimal to choose the one with the highest expected value (Glimcher, 2003; Gold and Shadlen, 2007). Neurons in the parietal and orbitofrontal cortex and also in the basal ganglia increase their activity for those stimuli that predict larger rewards or rewards that are delivered with a higher probability (Glimcher, 2003; Lau and Glimcher, 2008; Platt and Glimcher, 1999; Sugrue et al., 2004; van Duuren et al., 2009), and these structures may therefore play an important role in the coding of expected value as well as in the guidance of choice behavior.

Intriguingly, reward expectancy also influences neuronal activity in early visual cortex. Schuler and Bear (2006) demonstrated that neurons in rat primary visual cortex (area V1) 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 V1 neurons are usually thought to code low-level visual features rather than the value of stimuli. However, a recent study by Serences (2008) observed that reward expectancy also influences V1 activity in humans. In that study, subjects chose between two stimuli and if one of them was more rewarding than the other it evoked more activity. These results demonstrate that the effects of reward expectancy reach back to the earliest sensory processing levels, where they might influence the coding of low-level features. The precise mechanisms responsible for these reward
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effects, and in particular the relative importance of motivation and choice preference, has not yet been investigated.

Here we wished to gain insight into the effects of reward expectancy on neuronal activity in area V1 of macaque monkeys. Moreover, we aimed to investigate the relation between reward expectancy and attention (Maunsell, 2004). The effects of attention are as widespread across the brain as the effects of reward expectancy (Roelfsema, 2006; Schall and Thompson, 1999) but attention and reward expectancy have often been studied separately. It is plausible that reward and attention effects are related for at least two reasons. First, trials where high reward is at stake might cause a state of general attentiveness or arousal (Roesch and Olson, 2007). Second, reward expectancy might influence selective attention; in the presence of multiple stimuli, attention is likely to be attracted to those that are more rewarding (Maunsell, 2004). In area V1, the effects of selective attention usually do not occur during the initial response evoked by the presentation of a new stimulus, but after a longer delay (Roelfsema et al., 2003). The timing of the effects of reward expectancy on V1 activity is not yet known, but it could provide insight in the circuitry that is responsible for the reward expectancy effects.

We recorded neuronal activity in area V1 in a curve-tracing task in which two curves were associated with different rewards, and found that rewarding curves evoked stronger activity than unrewarding curves. Reward expectancy strongly influenced V1 activity if it biased the competition between curves, but variations in the overall reward expectancy had a weaker effect. This dependence of neuronal activity on the competition between stimuli is reminiscent of the effects of selective attention (Desimone and Duncan, 1995). Indeed, we found that the effects of reward expectancy had a similar timing and magnitude as the
effects of attention. Our results suggest that the explanatory frameworks employed by reward and attention studies provide converging accounts for a single neuronal selection mechanism at the level of the visual cortex.

RESULTS

We trained monkeys in a curve-tracing task where curves were associated with different rewards (Figure 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 monkeys directed their gaze towards a central fixation point and then two circular saccade targets and two curves appeared on the screen. Initially the monkeys did not know which curve had to be selected, but after 400ms the target curve was cued by the appearance of an additional contour segment that made a connection between this curve and the fixation point (‘connecting segment’ in Figure 1A). The monkeys had to make an eye movement to the circle at the end of the target curve. The critical manipulation was that the circular saccade targets had three possible colors that were associated with different reward magnitudes. A red circle indicated high reward (0.2ml fruit juice), yellow indicated medium reward (0.1ml) and green no reward. Saccades to the circle at the end of the distractor curve were counted as errors and were never rewarded. The monkeys learned to make 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 when the monkey had responded accurately to all stimuli.
Behavioral analysis

We first verified that the behavior of the monkeys was sensitive to the association between colors and rewards. A one-way ANOVA revealed a significant effect of the reward cues on the accuracy of both animals (Figure 1B,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 (Kawagoe et al., 1998b; Kobayashi et al., 2006; Milstein and Dorris, 2007; Takikawa et al., 2002), reward cues also influenced eye movements, which had a higher speed if a high-reward target curve was accompanied by a no-reward distractor than for the opposite combination (Figure 1B) (both monkeys, t-test, $p<10^{-3}$). Finally, reward cues influenced response times (RT). One monkey produced shorter RTs to curves associated with higher reward but effects of reward on average RT were less consistent in the other monkey (Figure S1). We did observe consistent effects on RT variability, which was lowest for the high-reward target curves (Figure 1B,C; paired t-test, Monkey A, $p<0.01$; Monkey G, $p<10^{-3}$). Thus, the animals were sensitive to the associations between colors and reward magnitudes.

Modulatory 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, the monkeys did not know which eye movement would be required so that the effects of reward value information on V1 activity are not influenced by eye movement planning. Because we presented two reward cues on every trial, we can distinguish between effects of overall reward expectancy and relative value. For the
definition of these quantities we followed Milstein and Dorris (2007) (see also Platt and Glimcher, 1999). The animal’s motivation during the initial stimulus epoch is expected to depend on overall reward expectancy, i.e. the average of the two possible rewards given that it is uncertain which curve will be cued:

\[ \text{Expected reward} = \sum_j P(C_{uj}) \cdot \text{reward}(C_{uj}) \]  

(1)

Here \( \text{reward}(C_{uj}) \) is the reward value associated with curve \( j \) and \( P(C_{uj}) \) is the probability that it will be cued (here 50% for either curve). In contrast, choice preference should depend on the relative value of one curve relative to the other one with a higher preference for curves that are more rewarding. The relative value of a curve \( C_{ui} \) is therefore defined as

\[ \text{relative value}(C_{ui}) = \frac{\text{reward}(C_{ui})}{\sum_j \text{reward}(C_{uj})} \]  

(2)

For example, if there is a curve with a red circle (0.2ml) and one with a yellow circle (0.1ml), the overall reward expectancy is 0.15ml because they are cued with equal probability, and the relative values are 0.67 and 0.33, respectively.

Figure 2A shows the position of the receptive field (RF) of an example V1 multi-unit recording site. We always configured the stimulus so that the RF fell on a curve segment between the colored circle and the connecting segment, thus assuring that RF stimulation was identical on every trial. Figure 2B illustrates how the response of the neurons depended on the colored reward cues (ANOVA in window from 200-450ms, \( F_{8,2713}=41.8; \ p<10^{-6} \)).
During the initial, transient phase of the 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 while 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 observed similar effects across a population of 41 V1 recording sites (29 in monkey A and 12 in monkey G). An ANOVA revealed a significant effect of the colored reward cues on activity ($F_{8,360} = 11.3, p<10^{-3}$) (Figure 2C,D). Neuronal activity was strongest if the RF-curve was associated with 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 relative value influenced V1 activity (yellow dashed line in Figure 2D). 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 (orange dashed line in Figure 2D). Accordingly, the correlation between V1 response strength and overall reward expectancy was weak (Figure 2E; $r=0.07; p>0.4$) whereas relative value was a good predictor of V1 activity (Figure 2F; $r=0.96; p<10^{-4}$). Control analyses demonstrated that differences in eye position between conditions were not responsible for the effects of reward expectancy (Supplementary Information).

**The relation between reward expectancy and selective attention**

Human observers solve the curve-tracing task by spreading visual attention over the target curve (Houtkamp et al., 2003) and previous studies have therefore attributed the modulation of V1 activity to attention shifts (Roelfsema, 2006). What is the relation
between attentional modulation caused by the central connecting segment, and the new effect of relative value on V1 activity? In Experiment 2 we used the same task, but introduced a second fixation delay of 400ms so that we could also monitor V1 activity after the target curve had been cued (Figure 3A). If there is a single, unified neuronal selection mechanism driven by reward information and selective attention, then (1) the neuronal effects of reward and attention cues should interact non-additively, and (2) neurons strongly influenced by reward cues should also be strongly affected by attention cues.

During the first delay (200-450ms) neuronal activity depended on relative value, just as in experiment 1 (ANOVA, $F_{8,378}=2.95$, $p<0.005$) (Figure 3B, left). 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 colors at the end of the curves lost their influence (Figure 3B, right). A two-way ANOVA with factors reward condition and target/distractor during the second delay (600-850ms) revealed a significant effect of target/distractor ($F_{1,756}=395$, $p<0.001$) but no effect of reward cues ($F_{8,756}=1.5$, $p>0.1$). Figure 3C 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 (red trace in Figure 3C), 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.
To investigate if the effects of the reward cues and the central attention cues are correlated across neurons, we calculated a reward modulation index ($M_{\text{Rew}}$) for every recording site in the first delay using conditions with the most extreme relative values $M_{\text{Rew}} = (R_{\text{High}} - R_{\text{No}})/(R_{\text{High}} + R_{\text{No}})$, and compared it to an attentional modulation index $M_{\text{Att}} = (R_{\text{T}} - T_{\text{D}})/(R_{\text{T}} + R_{\text{D}})$ during the second delay. We found a significant correlation between $M_{\text{Rew}}$ and $M_{\text{Att}}$ across recording sites in monkey A ($r=0.75$, $t_{29}=6.1$, $p<10^{-6}$) and monkey G ($r=0.59$, $t_{10}=2.3$, $p<0.025$). When we pooled data across the two monkeys after normalizing the range of modulation index values per monkey by computing Z-scores, the correlation coefficient was 0.71 ($t_{41}=6.4$, $p<10^{-6}$) (Figure 3D). This strong correlation indicates that reward and attention cues influence a corresponding population of V1 neurons.

To further investigate the relationship between the effect of reward cues and the central attention cues we determined the latency of these effects. To estimate the latency of the reward expectancy effect, we subtracted the average V1 response evoked by a curve with a low relative value ($G-R$ in Figure 2) from the response evoked by a curve with a high relative value ($R-G$) and fitted a curve to the response difference (Figure 4A,C). As a measure of latency we used the point in time where this fitted curve reached 33% of its maximal amplitude (this is arbitrary but we obtained similar results with other latency estimates, see Supplementary Information). The latency of the reward modulation was 118 ms (95%-confidence interval 98-128 ms). To measure the latency of the attentional modulation under comparable conditions, i.e. after the onset of a new stimulus, we carried out an additional experiment where the connecting segment (attentional cue) appeared at the same time as the visual stimulus (Figure 4B). Now the circles at the end of the two curves were grey and uninformative about reward value. The latency of the attentional response modulation was 119 ms (95%-confidence-interval 117-121 ms) (Figure 4D). The difference between the
latency of the attentional and reward modulation was not significant (P>0.1, bootstrap test). Thus, the effects of the colored reward cues and the central attention cues on neuronal activity in area V1 have a similar timing.

**Reward modulation is strongest in the presence of multiple curves**

Relative value and attention shifts cause similar modulation of V1 activity. Selective attention effects are most pronounced in the presence of competing stimuli (Desimone and Duncan, 1995) and we therefore tested if this also holds true for the reward cueing effects. In our final experiment (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 (Figure 5A). As in our previous experiments, we observed strong effects of relative value in the two-curve condition (Figure 5B). In the presence of a single curve, however, the effect of the reward cues was smaller and the activity evoked by high and no-reward curves was close to that evoked by the high reward curve of the two-curve condition. In the two-curve condition, the average $\text{MI}_{\text{rew}}$ 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 $\text{MI}_{\text{rew}}$ 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 4 to 5-fold stronger effect with two curves. Apparently, the effects of the reward cues on V1 activity are most pronounced in the presence of competing stimuli.
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DISCUSSION

We found that the relative value of a stimulus influences neuronal activity in area V1 during episodes when the monkey does not know which stimulus will have to be selected for a behavioral response. This result suggests that there is 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’ receptive fields on the contour element that was connected to the circle but not on the circle itself, which implies that the increased neuronal activity must have spread from the circle onto the curve and therefore suggests that reward information influences neuronal activity in an object-based manner. Effects of reward value have been reported previously for rat area V1 (Shuler and Bear, 2006) and also in human visual cortex with fMRI (Armony and Dolan, 2002; Serences, 2008; Serences and Saproo, 2010). The new findings 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 optimal choice behavior. At the same time, the effect of motivation as indexed by overall reward expectancy was relatively weak in V1. Comparable effects have previously been observed in area LIP (Dorris and Glimcher, 2004; Louie et al., 2011; Platt and Glimcher, 1999; Sugrue et al., 2004) and in premotor cortex (Pastor-Bernier and Cisek, 2011), 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 in economically optimal decision making (Cisek and Kalaska, 2010; Glimcher, 2003). Furthermore, the results establish a new link between the neuronal correlates of reward expectancy and object-based attention, cognitive functions that have often been studied separately in previous work.
The colored reward cues did not predict the position of the target curve, and their effect on the monkeys’ performance was counterproductive because they impaired accuracy. The monkeys could have increased their reward intake by ignoring the reward cues and focusing on the central connecting segment. Peck et al. (2009) recently reported a comparable maladaptive influence of reward cues in a task where monkeys saw a pre-cue informing them that a reward could be gained on that trial or not. If the cue predicted no reward, then the monkeys made inaccurate and slow eye movements to a saccade target appearing at the same location. Cues that predicted no reward evoked less activity in area LIP than cues signaling that the trial would be rewarding. The implication is that reward predicting stimuli are processed with priority over stimuli not associated with reward even if this prioritization process causes suboptimal task performance.

The relation between the effects of reward expectancy and attention on neuronal activity in the visual cortex has remained unclear in previous work (Maunsell, 2004). The present results demonstrate that reward predicting cues (Platt and Glimcher, 1999; Sugrue et al., 2004) and central cues used in studies of top-down attention (Roelfsema, 2006) (as opposed to stimulus-driven attention (Desimone and Duncan, 1995)) cause effects in area V1 that are comparable in several ways. First, the modulation of V1 activity induced by reward and attention cues has a similar latency of approximately 120 ms. Second, the modulation by reward expectancy is strongest in the presence of competing stimuli just as been observed for the effects of selective attention (Desimone and Duncan, 1995). Third, the strength of the response modulation caused by reward cues predicts the effect of attention cues across recording sites. Neurons with a strong effect of reward expectancy also tend to express a strong attention effect. Fourth, we observed little effect of reward cues after the
appearance of the central attention cue, which implies a non-additive, unitary effect of the two types of cues.

Why do reward-predicting cues and central ‘attention’ cues cause similar effects in V1? A possible explanation is inspired by the observation that the central cues also influence the reward expectancy 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 (Figure 6A). The finding that the central cues supersede the colored reward cues is therefore in accordance with an effect of relative value on activity in V1. A remarkable finding is that a target curve associated with no reward also evoked strong activity. We note, however, that this strong response 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 (Nakahara et al., 2004), the value of a zero-reward target curve is small but positive (\( \varepsilon \) in Figure 6B, see Methods 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 expectancy 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 in combination with previous studies (Dorris and Glimcher, 2004; Peck et al., 2009; Platt and Glimcher, 1999; Sugrue et al., 2004) inspire a unification of theories of selective attention and relative value coding. 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 (Maunsell, 2004). Vice versa, it is likely that studies on reward processing influence the distribution of selective attention across the stimuli in a display. Rewarding stimuli attract attention so that the visual cortex highlights stimuli with a high relative value (Peck et al., 2009), and the same holds true for stimuli that need to be processed to gain access to rewards (see e.g. Treue and Maunsell, 1996). The present results demonstrate that these attentional selection signals reflect the relative value of stimuli and suggest that there is a single, unified selection process at the level of the primary visual cortex. 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 V1 modulation depends on feedback from higher visual and perhaps frontal areas (Matsumoto et al., 2003; Padoa-Schioppa and Assad, 2006), which explains why it is 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.

EXPERIMENTAL PROCEDURES

We recorded neuronal activity from area V1 of two head-fixed monkeys with chronically implanted electrode arrays. Our procedures complied with the US National Institute of Health Guidelines for the Care and Use of Laboratory Animals and were approved by the institutional animal care and use committee of the Royal Netherlands Academy of Arts and Sciences of the Netherlands. 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 4x5 or 5x5 electrodes (Blackrock Inc.) with an impedance of 0.1-0.8MΩ (at 1 kHz) and a thickness of 80 μm were implanted chronically in area 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 (Roelfsema et al., 1998).

**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 (Figure 1A). A trial started as soon as the monkey’s eye position was within a 1.2°×1.2° window centered on a fixation point. After an interval of 300ms, the stimulus appeared on the screen. Both curves were initially not connected to the fixation point and they 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 (0.2ml), an intermediate amount (0.1ml) and no fruit juice, respectively. The monkeys had to maintain fixation for 400ms, and then a ‘connecting segment’ appeared that attached the target curve to the fixation point. In Experiment 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 400ms after the appearance of the connecting segment. In Experiments 1 and 2 there were a total of 18 conditions because we crossed the 9 possible combinations of two colored circles with two connecting segments. In Experiment 3 there were 6 conditions. Four of these had two curves, one of which was associated with a high reward and the other with no reward (2 stimuli) crossed with cueing of either the high reward or the no reward curve (2 cuing conditions). The other two conditions had a single curve associated with high or no reward,
and this curve was always cued. In all experiments the stimuli were randomly interleaved and they 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 (Figure 1), we used data from 6 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**

Spiking activity was recorded from the chronically implanted multi-electrode arrays with TDT (Tucker Davis Technologies) recording equipment. As in previous studies (Logothetis et al., 2001; Pooresmaeili et al., 2010; Supèr and Roelfsema, 2005; Xing et al., 2009), the MUA signal was amplified, band-pass filtered (300-9000Hz), full-wave rectified, low-pass filtered (<200Hz) and sampled at a rate of 763Hz. MUA recorded in this manner gives an instantaneous measure of spiking activity of neurons around the electrode tip. We have compared MUA to single-unit data in the curve-tracing task (Pooresmaeili et al., 2010; Supèr and Roelfsema, 2005) and found that it yields a reliable estimate of the average single-unit response (also see Cohen and Maunsell, 2009). The receptive field dimensions were estimated using the onset and offset of the visual response to a slowly moving white bar on a black background, in each of eight possible directions (Supèr and Roelfsema, 2005). The median area of the receptive fields was 0.52 deg² (ranging from 0.1 deg² to 2.4 deg²). Receptive field eccentricity ranged from 1.2° to 5° with an average of 3.1°.

We computed peri-stimulus time histograms in a time window ranging from 300 ms before stimulus onset until 500-800ms afterwards and normalized activity to the peak response.
after subtraction of the spontaneous activity (average activity in a 100 ms window before
stimulus onset). The peak response was determined as the maximal activity in an interval
between 0 and 150 ms after stimulus onset. The responses were smoothed with a Gaussian
kernel with an s.d. of 13 ms. The method used to determine the latency of the reward
modulation and the attentional modulation is described in Supplementary Information.

**Definition of relative value and modulation index**

Relative value was defined as in equation 2. It is not well defined for a stimulus with two
green circles (division by zero), unless we assume that there is a residual value \( \varepsilon \) associated
with a correct response because it gives access to later trials where larger rewards can be
gained (Figure 6B). To make the regressions in Figure 2E,F we used an \( \varepsilon \) of 0.01 ml so that
the value of a red, yellow and green circle became 0.21, 0.11 and 0.01 ml juice, respectively.
We investigated how strongly our results depended on this particular choice of \( \varepsilon \), and found
that other values within a wide range yielded virtually identical results. The \( \varepsilon \) of 0.01 used by
us resulted in an \( r \) of 0.96 for the correlation between V1 activity and relative value (Figure
2F); \( r \) was 0.95 or 0.96 if we used an \( \varepsilon \) of 0.001 or 0.02, respectively.

We computed modulation indices \( M_{\text{Rew}} \) and \( M_{\text{Att}} \) to measure the response modulation
induced by relative value and selective attention, respectively. \( M_{\text{Rew}} \) was defined as:

\[
M_{\text{Rew}} = \frac{(R_{\text{High}} - R_{\text{No}})}{(R_{\text{High}} + R_{\text{No}})}
\]

(3)

Here \( R_{\text{High}} \) denotes the response evoked by the high reward curve if a no reward curve was
placed outside the RF, while \( R_{\text{No}} \) denoted the response evoked by the no-reward curve in
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the presence of a high-reward curve outside the RF. The attentional modulation index was defined as:

$$MI_{\text{Att}} = \frac{R_T - R_D}{R_T + R_D}$$

(4)

where $R_T$ and $R_D$ denote responses evoked by the target and distractor curve, respectively. To analyze the correlation between $MI_{\text{Rew}}$ and $MI_{\text{Att}}$ across monkeys (Figure 3D), we computed Z-scores per monkey by subtracting the mean MI and then dividing by the standard deviation across recording sites.

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Figure 1 Effects of reward expectancy 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=0ml, yellow=0.1ml, red=0.2ml 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 panel), eye speed (middle) and variability in response time (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 s.e.m.

(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.
Figure 2 Effect of reward information on neuronal activity in area V1

(A) Example stimulus and receptive field 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
(nRF; not in the RF). (C) Activity averaged across the population of 41 recording sites in the two monkeys.

(D) Average activity in a window from 200-450ms after stimulus onset as function of the color of the circle at the end of the RF and nRF-curve. Error bars represent s.e.m. The yellow dashed line connects conditions with varying relative value but constant overall reward expectancy (0.1ml), whereas the orange line connects conditions with varying reward expectancy but constant relative value (0.5).

(E,F) Neuronal activity as function of the overall reward expectancy (E) and relative value (F).

$r$ denotes correlation coefficient.
Figure 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 panel shows neuronal activity in the first delay and right panel activity in the second delay. Error bars, s.e.m.
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(C) The average activity in the conditions with maximal and minimal relative value during the first delay. Insets denote conditions and position of RF (grey square).

(D) Correlation between the Z-scores of the attention (abscissa, $M_{\text{Att}}$) and reward modulation index (ordinate, $M_{\text{Rew}}$). Red data points are from monkey A ($N=29$) and green data points from monkey G ($N=12$).
Figure 4 Comparison of the latency of attentional and reward modulation

(A) The latency of the reward cueing effect was estimated from the two conditions of Experiment 1 where the curve in the RF had a maximal or minimal relative value.

(B) Additional experiment where the target curve was cued by the connecting segment as soon as the stimulus appeared and the circles were grey and uninformative about reward value.

(C) The latency of the reward effect was estimated by fitting a curve to the difference in activity evoked by curves with a maximal (R-G) and minimal (G-R) relative value. The black bar on the X-axis denotes the 95%-confidence interval of the latency of the reward modulation.
(D) The latency of the attentional modulation was measured by subtracting the response evoked by the distractor curve from the response evoked by the target curve.
Figure 5 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).
Figure 6 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 $\varepsilon$ because it provides access to future trials where real rewards can be gained. Therefore the relative value of a target curve with a green circle equals 100% (lower panel).


Chapter 3


