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Rewarding Feedback After Correct Visual Discriminations Has Both General and Specific Influences on Visual Cortex

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Weil RS, Furl N, Ruff CC, Symmonds M, Flandin G, Dolan RJ, Driver J, Rees G. Rewarding feedback after correct visual discriminations has both general and specific influences on visual cortex. *J Neurophysiol* 104: 1746–1757, 2010. First published July 21, 2010; doi:10.1152/jn.00870.2009. Reward can influence visual performance, but the neural basis of this effect remains poorly understood. Here we used functional magnetic resonance imaging to investigate how rewarding feedback affected activity in distinct areas of human visual cortex, separating rewarding feedback events after correct performance from preceding visual events. Participants discriminated oriented gratings in either hemifield, receiving auditory feedback at trial end that signaled financial reward after correct performance. Greater rewards improved performance for all but the most difficult trials. Rewarding feedback increased blood-oxygen-level-dependent (BOLD) signals in striatum and orbitofrontal cortex. It also increased BOLD signals in visual areas beyond retinotopic cortex, but not in primary visual cortex representing the judged stimuli. These modulations were seen at a time point in which no visual stimuli were presented or expected, demonstrating a novel type of activity change in visual cortex that cannot reflect modulation of response to incoming or anticipated visual stimuli. Rewarded trials led on the *next* trial to improved performance and enhanced visual activity contralateral to the judged stimulus, for retinotopic representations of the judged visual stimuli in V1. Our findings distinguish general effects in nonretinotopic visual cortex when receiving rewarding feedback after correct performance from consequences of reward for spatially specific responses in V1.

INTRODUCTION

Reward can influence performance and brain activity on tasks requiring sensory discrimination. For instance, in somatosensory discrimination tasks, rewarding feedback received after correct sensory discrimination can modulate primary somatosensory cortex activity in humans (Pleger et al. 2008) with related findings in other mammals (Pantoja et al. 2007). But it is less clear whether (and how) rewarding feedback can modulate activity associated with visual discriminations in visual cortices. In humans, there is now some evidence that activity in visual cortex can be enhanced by anticipatory reward expectation (Krawczyk et al. 2007; Small et al. 2005) or motivation (Engelmann et al. 2009) and may track the value of visual stimuli during decision tasks (Serences 2008). Monetary incentive has also been shown directly to enhance visual detection sensitivity (Engelmann and Pessoa 2007). But such recent work either did not assess how reward for performance in perceptual tasks affects distinct identified areas within visual cortex (including retinotopically mapped regions) (Krawczyk et al. 2007; Small et al. 2005) or did not dissociate possible modulatory effects of reward or object value on visually evoked responses versus any impact of receiving rewarding feedback *independent* of visual stimulation (Serences 2008).

We used 3T functional magnetic resonance imaging (fMRI) in humans to examine whether and how rewarding feedback given *after* correct performance on a visual discrimination task influenced blood-oxygen-level-dependent (BOLD) signals in different visual areas. We required participants to discriminate the orientation of two achromatic gratings presented successively in one visual field, while ignoring similar (but independently oriented) gratings in the other visual field. By analogy with a recent somatosensory study (Pleger et al. 2008), participants received feedback indicating financial reward for each correct judgment only at trial end as signaled here by *auditory* feedback. In contrast to previous studies on the effects of reward or value on visual task performance and brain activity (Krawczyk et al. 2007; Serences 2008; Small et al. 2005), our event-related fMRI design allowed us to distinguish temporally those BOLD signals associated with visual discrimination of the gratings from those attributable to subsequent nonvisual rewarding feedback. This temporal separation made it possible to examine effects of rewarding feedback on visual cortex activity *after* the corresponding visual discrimination had been completed. Any effects on visual cortex activity at this rewarding-feedback stage of the trial thus could not reflect standard enhancements of task-related visual processing by spatial attention as the task-related visual stimuli had long since disappeared (see following text). We used retinotopic mapping of early visual areas V1–V3, identifying lateralized representations of the visual targets within these areas so that we could specifically assess any impact of rewarding feedback for retinotopic representations of the preceding stimuli as well as for higher areas of visual cortex.

To anticipate, visual cortex beyond retinotopic regions showed increased BOLD signals during (nonvisual) rewarding feedback, whereas early retinotopic visual cortex showed instead enhanced BOLD signals in response to the judged visual grating on the *next* trial, after receipt of rewarding feedback on the previous trial. Thus higher-level areas in visual cortex and early retinotopic regions show distinct patterns of influence at different phases of task performance. The brain response to rewarding feedback was clearly distinct from well-known effects of spatial attention present during visual discrimination. Together our results suggest a new mechanism by which rewarding feedback may affect visual cortex to aid subsequent visual processing.

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METHODS

Participants

Twelve neurologically normal right-handed adults (20–32 yr old, 5 females), with normal or corrected vision by self-report, gave written informed consent to participate in the study, which was approved by the local ethics committee.

Stimuli

Each visual display (see Fig. 1*A*) comprised two achromatic circular grating patches drawn from a set of similar gratings (see following text). Each patch subtended 4° in diameter (spatial frequency: 3 cycle/°, luminance: 0.10–13.64 cd/m^2) presented in the left and right upper quadrants (1 grating in each quadrant), at an eccentricity of 6.41° (5° along the horizontal meridian, 4° vertically). The background was a uniform gray screen of luminance 3.66 cd/m^2. A central fixation point (black square measuring 0.4° diam, luminance: 0.10 cd/m^2, with central white square, 0.2° diameter, luminance: 13.64 cd/m^2) was present throughout the experiment.

The stimulus set comprised 10 different gratings orientated in steps of 1° (4 subjects) or 2° (8 subjects) away from vertical in either the clockwise or anticlockwise direction. Differences in orientation were determined on a per-participant basis to match individual performance levels by means of pilot testing implemented as a practice session in the scanner (without financial reward). Participants could only proceed to the main experiment if they achieved an accuracy of ~75% correct responses. The task was made easier or more difficult using larger or smaller orientation differences according to the participant's individual score during this initial piloting and preselection.

Stimuli were projected using an LCD projector (NEC LT158, refresh rate: 60 Hz, screen resolution: 640 × 480) onto a circular

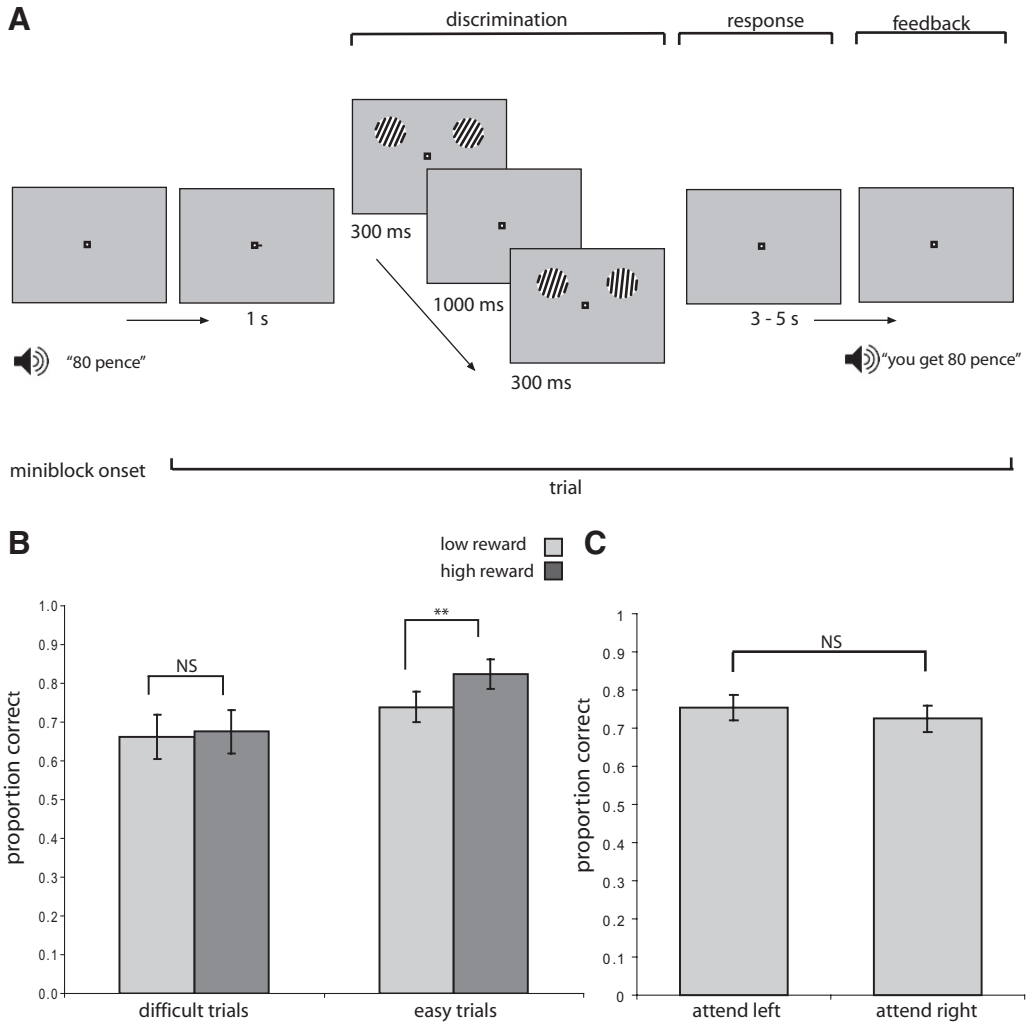

FIG. 1. Procedure and behavioral findings. *A*: trials were grouped into short "mini-blocks" of 4 with 2 possible reward levels: 10 or 80 pence per correct discrimination. At the onset of each mini-block, participants heard an auditory cue informing them of the reward level for that mini-block. The onset of each trial began with a small visual precue directing participants to attend covertly to either the left or right grating. Attended side remained constant throughout the mini-block. This was followed by the visual stimuli to discriminate: participants fixated centrally while attending to one side and were shown bilateral gratings for 300 ms, followed by a uniform gray screen, and then a further pair of bilateral gratings with different orientations. The task was to decide, for the attended side only, which display (1st or 2nd) contained the grating with the more vertical orientation. Participants were given 3–5 s to respond using a key press. This was followed by auditory feedback, informing participants of the amount won for a correct response, e.g., "you get 80 pence," or for an incorrect response: "you get 0 pence." Jittering the separation of reward feedback from the discrimination task, together with the different levels of reward and the rewarded or no-reward outcome, allowed us to dissociate hemodynamic responses that were specific to the feedback of reward from responses associated with the visual discrimination (see main text). The inter-trial interval was 3–5 s. *B*: higher reward levels were associated with improved accuracy in the visual discrimination task for the easier but not the hardest trials. *C*: there were no differences in accuracy for visual discrimination of gratings attended in the left or right hemifields. Error bars = 1 SE of the difference between paired conditions. **, statistical significance ($P < 0.05$, 2-tailed paired *t*-test), NS, not significant.

projection screen at the rear of the scanner. Participants viewed the screen via a mirror positioned within the head coil. All stimuli were presented via MATLAB 6.5.1 (Mathworks), using the COGENT 2000 toolbox (www.vislab.ucl.ac.uk/Cogent2000/index.html). Auditory stimuli were recorded using a Behringer two channel mixer (// www.behringer.com) and presented using COGENT via etymotic headphones.

Procedure

Participants performed a temporal two-alternative forced-choice orientation-discrimination task (Fig. 1*A*). On each trial, a pair of gratings was presented in the upper left and right visual fields for 300 ms, followed after an interval of 1,000 ms by a second pair of gratings presented at the same location for 300 ms (see Fig. 1*A*). Participants were required to fixate centrally while attending either the upper-left or upper-right location to discriminate which of the two gratings presented successively at that location (1st or 2nd) was oriented closer to vertical. Three to 5 s after presentation of the second grating (randomly jittered), participants received *auditory feedback* indicating the amount won. This consisted of a recorded female voice informing them "you get 10 pence" or "you get 80 pence" following a correct discrimination, depending on the reward magnitude for that block, or "you get zero pence" for an incorrect discrimination. Each type of auditory feedback took 1,902 ± 1.3 (SE) ms to play. Thus the visual discrimination phase of the trial, when the gratings were presented, was separated from the later reward-phase of the trial, when only auditory feedback was given. We decorrelated BOLD signal attributable to reward-phase feedback from that due to the preceding visual stimulus presentation by including a temporal jitter of 3–5 s between visual stimulus and reward administration, by using different reward levels, and by titrating task difficulty to yield 60–80% correct responses (and hence a sizeable proportion of trials with no-reward feedback). The inter-trial interval was 3–5 s, again randomly jittered. Every correct response was followed by reward and every incorrect response by nonreward (0 pence), to maximize the incentive to perform the visual task correctly, and in accord with previous research in related paradigms (Della and Chelazzi 2006; Leon and Shadlen 1999; Maunsell 2004; Pleger et al. 2008).

On each trial, the orientation of the first grating on the attended side was chosen randomly from the pool of possible orientations for that subject (see stimulus description in the preceding text). The second grating on that side was chosen from the remainder of the stimulus set with the same direction of rotation. Thus both gratings on one side were always oriented in either a clockwise direction, or an anticlockwise direction, for any one trial. But the difference in orientation between the two successive gratings could vary with two levels of discrimination difficulty. Our stimuli consisted of easy (2–8° difference in orientation) and difficult discriminations (1–2° difference in orientation), titrated according to individual participants' ability, with equal numbers of trials in each type (easy or difficult). The orientation of the gratings in each hemifield was always different but otherwise independent. The difficulty factor was randomly assigned for each trial within a block.

We investigated two magnitudes of possible financial reward: 10 or 80 pence for each correct discrimination. Each magnitude was tested for each hemifield over 40 trials in total for each participant. Four successive trials of a particular reward magnitude were grouped into mini-blocks, otherwise randomly determined. Each such mini-block also included one "rest" trial of exactly the same duration as normal trials (7.5 −9.5 s, varying due to jitter). Rest trials consisted of only a uniform gray screen (luminance: 3.66 cd/m^2) with a central fixation point but no gratings and no auditory feedback. The sequential position of the rest trials within each mini-block was assigned randomly.

The onset of each mini-block was signaled by an auditory cue ("10 pence" or "80 pence"), indicating the level of reward for each correct discrimination within that mini-block. This was followed by a visual precue directing participants to attend to either the left or right grating for all of the subsequent trials in that mini-block. This visual precue consisted of a small black horizontal bar (0.2 × 0.1°, luminance: 0.10 cd/m^2) immediately to either the left or right side of the fixation point. The onset of the trial began 1 s after the auditory cue.

Gratings were always presented in both the right and left hemifield, but participants were directed to attend covertly only to the one side that had to be judged (and was rewarded for a correct discrimination) in a given mini-block, by the small visual precue bar at the start of each such mini-block (see preceding text), with side of covert attention decided randomly for each block. The brief grating presentations, at unpredictable orientations, minimized any visual aftereffects. Participants indicated their judgment using one or other of two possible button presses with their right hand.

Participants were reimbursed for participation according to the summed reward across 50% of randomly chosen trials after scanning. Thus the financial rewards were real.

fMRI scanning

A 3T Siemens Allegra system acquired T2*-weighted echo planar (EPI) images with BOLD contrast. T1-weighted anatomical images were acquired using a 1.5T Siemens Sonata system. Each EPI image comprised 40 3-mm axial slices covering the whole cerebrum with an in-plane resolution of 3 × 3 mm. The main experiment was split into five runs, each consisting of 243–260 volumes (duration of the run differed slightly between participants due to the jittering between stimulus presentation and feedback and the intertrial jittering). The first 5 volumes of each run were discarded to allow for T1 equilibration effects. Volumes were acquired continuously with a TR of 2.4 s/volume.

The main experiment was followed by four further functional imaging runs to independently functionally localize the retinotopic representations of the peripheral gratings in particular, for subsequent region-of-interest (ROI) analyses (see following text). Participants fixated centrally while viewing a circular checkerboard the same size and location as each grating in the main experiment (4° diam at 6.41° eccentricity, 5° across, 4° up), contrast-reversing at 10 Hz on a uniform gray background (luminance 3.66 cd/m^2); see Supplementary Fig S1*C*.[1] This checkerboard stimulus was presented for 5 volumes on either side, interleaved with rest periods lasting for 3 volumes with a uniform gray screen and no checkerboard displayed. That whole sequence was then repeated eight times for each stimulus localizer run. A central fixation point was present throughout, with fixation confirmed by eye-tracking, as for the main experiment also (see following text). This stimulus localizer procedure comprised 140 volumes in total, with fMRI sequence and parameters identical to the main experiment. This was followed by two further runs to localize functionally the borders of retinotopic visual areas V1, V2 and V3. Flashing checkerboard patterns covering either the horizontal or vertical meridian (see Supplementary Fig S1*A*) were alternated with rest periods for five epochs of 10 volumes over two scanning runs, each lasting 155 volumes.

Finally, a Siemens standard double-echo gradient-echo field map sequence was acquired for distortion correction of the EPI images. (echo times: 10.0 and 12.46 ms, TR = 1,020 ms, matrix size = 64 × 64, 64 slices covering the whole head, voxel size = 3 × 3 × 3 mm).

Eye tracking

During scanning, eye position and pupil diameter were continually sampled at 60 Hz using long-range infrared video-oculography (ASL 504LRO Eye Tracking System, accurate to within 0.5 visual degrees) to ensure participants maintained fixation. Eye position was monitored

[1] The online version of this article contains supplemental data.

on-line via a video screen, for all participants, and this confirmed good adherence to the fixation requirement. Eye position was recorded to disk and subsequently analyzed for six participants (see following text) but was not stored for the other six due to technical problems.

fMRI whole brain analyses

Functional imaging data were analyzed using Statistical Parametric Mapping software (SPM5, Wellcome Trust Centre for Imaging Neuroscience, University College London). EPI images were corrected for geometric distortions caused by susceptibility-induced field inhomogeneities. A combined approach was used that corrects both for static distortions and changes in these distortions due to head motion (Andersson et al. 2001; Hutton et al. 2002). The static distortions were calculated for each participant by processing the field map, using the FieldMap toolbox implemented in SPM5. The images were then realigned and unwarped using SPM5 (Andersson et al. 2001), using procedures that allow the measured static distortions to be included in the estimation of distortion changes associated with head motion. Images were then spatially normalized to the standard template for the Montreal Neurological Institute (MNI), using the unified segmentation algorithm in SPM5 for spatial normalization and smoothed with a Gaussian kernel (Full Width Half Maximum 10 mm), in accord with the standard SPM approach.

Trial-specific regressors were created by generating delta functions that represented trial onsets for each of the combinations of attended hemifield (left or right) and reward magnitude (high or low) during the visual phase of each trial; and for each of the combinations of attended hemifield (left or right), reward magnitude (high or low), and whether or not reward was given for the feedback phase. These were convolved with a synthetic hemodynamic response. In addition, rest trials were modeled for both the visual- and feedback phases to reduce residual error in the estimation of the event-related hemodynamic response function (Dale 1999). Motion parameters defined by the realignment procedure were employed as six separate regressors of no interest. Data were high-pass filtered (cut-off: 0.0078 Hz) to remove low-frequency signal drifts; the regressors were then entered into a multiple linear regression model, and parameter estimates determined for all brain voxels.

Appropriately weighted linear contrasts were conducted between the experimental conditions of interest, and corresponding parameters estimated on a voxel-wise basis. The resulting set of t values constituted a statistical parametric map (SPM{T}), which was assessed in two different ways. For the whole brain analyses, where we had a prior hypothesis we used appropriate small volume corrections [SVCs, using a threshold of $P < 0.05$ corrected for multiple comparisons across the small volume examined, (Worsley 2003) based on the PickAtlas (//www.fmri.wfubmc.edu/cms/software#PickAtlas] to independently define anatomical regions of interest. These comprised subcortical areas previously described as being activated by reward (specifically ventral striatum) (Elliott et al. 2000; Knutson et al. 2001; O'Doherty et al. 2001); plus areas known to be activated by visual stimuli (specifically, the occipital lobe). For all other areas, we used a more conservative correction across the whole brain volume at a cluster threshold of $P < 0.05$, family-wise error corrected.

fMRI retinotopic analyses

In addition to whole-brain group analyses, we also examined activation within retinotopic ROIs in early visual cortex, corresponding to the visual field locations of the visual stimuli as separately localized. In accord with standard practice, these analyses were carried out on an individual-participant basis without spatial normalization and with a correspondingly smaller degree of spatial smoothing. Image volumes for each participant were realigned spatially to the first volume, and resulting image volumes were coregistered for each participant to their own structural scan and smoothed with a Gaussian kernel (FWHM 6 mm) to improve signal to noise. Trial-specific regressors were generated using the same procedure as in the whole brain analysis, followed by multiple linear regression (using SPM5, as in the preceding text) to produce voxel-wise estimates of activation for each experimental condition.

To identify the boundaries of retinotopic visual cortices V1–V3, standard retinotopic mapping procedures were used (Sereno et al. 1995; Teo et al. 1997; Wandell et al. 2000). SPM5 was used to generate activation maps for the horizontal and vertical meridians. Mask volumes for each ROI were obtained by delineating the borders between visual areas using activation patterns from the meridian localizers. We followed standard definitions of V1–V3 together with segmentation and cortical flattening using Freesurfer (http://surfer.nmr.mgh.harvard.edu/). Note that for all ROI analyses, only 11 (of a total of 12) participants were included as 1 participant had moved between the main functional experiment and the localizer experiment such that their occipital pole was mislocated and lay outside the range of the main scanned volume.

The mask volumes for V1–V3, in conjunction with the functional localizer images for stimulus-responsive regions, were used to identify voxels showing significant activation ($T = 2.5$, with some variability across participants to ensure contiguous collection of voxels) for the comparison of trials where the target localizer was present, compared with rest periods, using the regression analysis described in the preceding text. This comparison identifies voxels activated by the grating stimulus in each of the retinotopic areas as determined by the independent meridian mapping procedure. The final analytic step was to extract from these independently defined ROIs the regression parameters for each experimental condition arising from the analysis of the main experimental time series. These were averaged across voxels in V1, V2, or V3 that responded to the visual field location corresponding to the gratings for every participant, then averaged across participants, yielding estimates of mean percentage signal change for each condition.

The statistical significance of any differences in activation during the main experiment within the ROIs defined by the independent localizer scans was assessed with separate repeated-measures ANOVAs with condition (attended side, reward level, reward received or not) as repeated factor for each of the ROIs in V1, V2, and V3 separately.

Eye-tracking analysis

Eye-tracking data recorded during scanning were analyzed with MATLAB 7 (Mathworks, Sherborn, MA). Blinks and periods of signal loss were removed from the data. Eye position in the horizontal and vertical directions relative to fixation and any tendency for eye movements (assessed via the SD around the mean eye position) were then computed separately for the visual- and reward-feedback phase of each trial within each condition. A positive value in the horizontal direction indicated a shift into the right hemifield. A repeated-measures ANOVA, was used to establish whether mean eye position or its SD differed between experimental conditions.

RESULTS

Behavioral data

Increased monetary reward was associated with improved accuracy of visual discrimination for easier trials [$t(11) = 2.3$, $P = 0.048$] but not for the most difficult trials where the difference in orientation between successive gratings was smallest [$t(11) = 0.46$, $P = 0.65$; see Fig. 1*B*]. The accuracy of visual discrimination did not differ between right and left hemifields [$t(11) = 0.87$ $P = 0.44$, NS; see Fig. 1*C*].

We also considered how receiving rewarding feedback after correct performance on a given trial might affect discrimination accuracy on a subsequent trial (Pleger et al. 2008, 2009). We found a tendency for an increase in the conditional probability of the next trial being correct after receiving reward on the previous trial, compared with not receiving a reward on a previous incorrect trial [$t(11) = 1.9$, $P = 0.051$, 1-tailed; see leftmost two bars in Fig. 4*A*]. This pattern did not significantly differ for higher versus lower rewarded trials [$F(1,11) = 0.11$, $P = 0.75$, NS].

Next we examined whether this trial-to-trial effect was specific to immediately successive pairs of trials, or instead might reflect more extended "clusters" of good performance after receiving rewarding feedback for correct performance (as might be expected if there were slow fluctuations in alertness or other nonspecific factors). In addition to examining the proportion of correct responses when the immediately preceding trial ($n - 1$) received rewarding feedback after correct performance, we examined the proportion of correct trials when the $n - 2$ and $n - 3$ trials were rewarded for correctness. We found that the trial-to-trial effect was lost for these earlier trials: $t(11) = 0.21$, $P = 0.42$, for the one-tailed t-test comparing proportion correct in trials where the $n - 2$ trial received rewarding feedback versus did not; $t(11) = 0.91$, $P = 0.19$, for the one-tailed t-test comparing proportion correct in trials where the $n - 3$ trial received rewarding feedback or did not. Our behavioral data are thus consistent with a specific effect from one trial to the next rather than a more general change in some longer-lasting state of vigilance or arousal.

fMRI data

We performed three related sets of analyses on the fMRI data. These focused on the visual discrimination phase of each trial, on the reward feedback phase, or on trial-to-trial effects. In each case, we report ROI-based results in retinotopic visual cortical areas V1-V3 first, followed by results from the whole-brain analyses outside these retinotopic areas.

VISUAL DISCRIMINATION PHASE. The visual discrimination phase consisted of presentation of lateralized grating stimuli, one of which (the attended side) was discriminated. No reward feedback (neither for correct nor incorrect trials) was presented during this phase although it would be possible to anticipate the overall level of reward at stake because participants were aware of whether each trial was in a high or low reward miniblock as signaled at the start of each miniblock. We anticipated finding the standard retinotopic effects of spatial attention in visual cortex for our ROI-based analyses within the visual discrimination phase with increased activity contralateral to the attended side for ROIs within V1–V3, but no effect of future reward feedback (i.e., correct vs. incorrect trials) and had no specific hypotheses regarding possible effects of reward-level anticipation.

Comparing the effect of attending to the left or right grating revealed as expected a main effect of spatial attention for contralateral (vs. ipsilateral) attention in the retinotopic representations of the stimulus location in V1 [$F(1,10) = 16.0$, $P = 0.003$], V2 [$F(1,10) = 19.3$, $P = 0.001$], and V3 [$F(1,10) = 26.1$, $P < .005$); see Fig. 2]. This is consistent with numerous previous findings (e.g., (Buchel et al. 1998; Kastner et al. 1999; Martinez et al. 1999; Silver and Kastner 2009; Silver et al. 2007). There were no effects of contralateral (vs. ipsilateral) attention outside retinotopic cortex on whole-brain analysis (all $P > 0.05$, corrected for multiple comparisons).

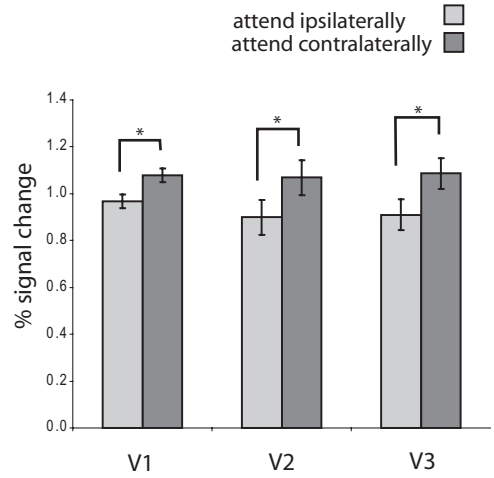

FIG. 2. Differences in brain activity during visual discrimination. Blood-oxygen-level-dependent (BOLD) signal change (percent relative to the global mean) averaged across 11 retinotopically mapped participants, for the regions of interest (ROIs) responding to the grating stimuli in V1–V3 during the visual-discrimination phase of the trial. Responses are plotted separately for gratings attended in the contra- or ipsilateral hemifields. Error bars are SE of the difference between paired conditions; *, statistical significance ($P < 0.05$, 2-tailed paired t-test).

During the discrimination phase of the trial, participants had not yet been informed whether they were correct (or not) and thus whether they would receive a reward on that trial. Consistent with this, we did not detect any differences in activity (all $P > 0.4$ in retinotopic ROIs) evoked in the discrimination phase on trials that would later be rewarded (i.e., were correctly judged) versus not rewarded (i.e., incorrect). For V1: $F(1,10) = 0.58$, $P = 0.46$; V2: $F(1,10) = 0.67$, $P = 0.43$; V3: $F(1,10) = 0.42$, $P = 0.53$.

Similarly, there were no significant differences in activity in visual cortex on whole-brain analysis outside retinotopic visual cortex (all $P > 0.1$, corrected) for this contrast in the visual-discrimination-phase. This lack of difference between correct and incorrect trials during visual discrimination suggests that any differences between BOLD signals for rewarded versus not-rewarded trials that might arise at the later time point of rewarding feedback (see following text) would be unlikely to reflect differences in spatial attention during the visual discrimination itself.

Finally, we identified any significant differences in brain activity during the discrimination phase for blocks where receiving higher reward (80 pence) compared with lower reward (10 pence) was possible. Note that at this point, participants had not yet received reward feedback, so the comparison is between the anticipation of higher versus lower reward, irrespective of whether reward was eventually received. In retinotopic ROIs, there was no main effect of anticipated reward-level in V1, [$F(1,10) = 2.0$, $P = 0.19$], but there was a main effect of reward- level in V2 [$F(1,10) = 5.7$, $P = 0.038$] and a trend in V3 [$F(1,10) = 3.5$, $P = 0.09$]. The absence of an anticipated reward-level in V1 might reflect some difference between visual areas, or (as with all null outcomes in fMRI) potentially a lack of statistical power.

Outside retinotopic cortex, whole-brain analysis revealed significant activation for blocks with higher minus lower reward-levels anticipated, within ventral striatum (coordinates [−12 20 0], $t = 4.22$, $P = 0.039$ small-volume corrected), left superior temporal gyrus [coordinates [−60, 12, 2], $t = 5.37$, $P < 0.005$ family-wise error (fwe)-corrected], left cingulate gyrus (coordinates [−8, 18, 42], $t = 5.21$, $P = 0.005$ fwe-corrected), and right inferior frontal gyrus (coordinates [48, 26, −6], $t = 4.56$, $P = 0.025$ fwe-corrected).

Finally there was also an interaction between easy versus hard difficulty level and reward level in V1 [$F(1,10) = 5.1$, $P = 0.048$], resembling the interaction observed in our behavioral data (see Fig. 1*B*), although this interaction was not found significantly in V2 [$F(1,10) = 1.6$, $P = 0.23$] or V3 [$F(1,10) = 2.73$, $P = 0.13$]. This interaction reflects a stronger impact of higher anticipated reward in V1 for the easier trials (that were affected behaviorally by reward level).

Taken together, these findings from the visual discrimination-phase indicate the expected modulations of stimulus representations in visual cortex by spatial attention during the discrimination, consistent with many previous studies (Kastner et al. 1999; Martinez et al. 1999); plus some modulation of retinotopic visual cortex by anticipated reward value, potentially consistent with recent studies examining motivational effects of reward (Engelmann et al. 2009; see also Serences 2008). But we found no evidence for any difference between correct (rewarded) and incorrect (nonrewarded) trials at the point of discrimination within visual cortex.

REWARD FEEDBACK PHASE. We next examined the effect of rewarding feedback during the (nonvisual) reward-feedback phase of each trial. Note that during this phase of the trial, participants were given auditory feedback via headphones while viewing a gray screen (present throughout the experiment) but were not shown any visual stimuli. Our specific interest in these analyses focused on any differences between correct (rewarded) and incorrect (not-rewarded) trials that now became apparent to participants at this nonvisual phase of the trial, plus any effects of the level of reward (high vs. low) when actually received via the feedback.

In retinotopic cortex, stimulus-responsive ROIs did not show any significant main effect of receiving reward (vs. no reward) feedback (on correct vs. incorrect trials, respectively) in V1, V2, or V3 [V1: $F(1,10) = 0.86$, $P = 0.38$; V2: $F(1,10) = 0.98$, $P = 0.35$; V3: $F(1,10) = 0.005$, $P = 0.95$; see leftmost three bars in Fig. 3*B*]. There was also no main effect of

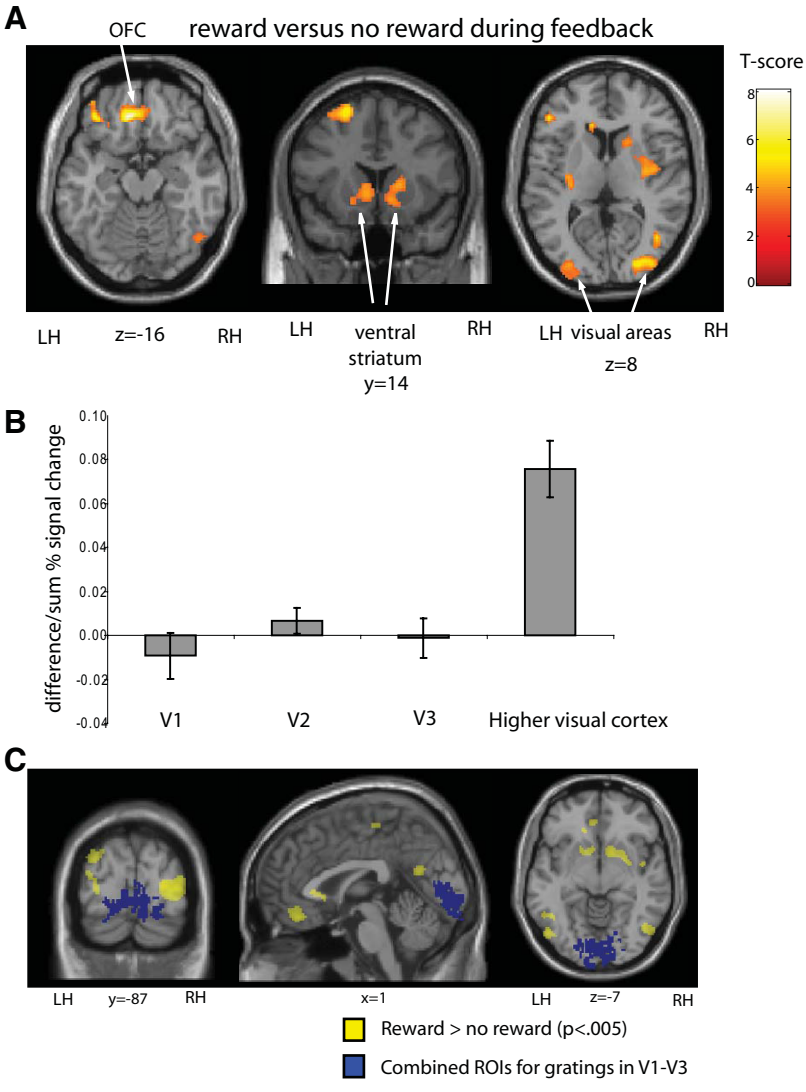

FIG. 3. Changes in brain activity during reward feedback. *A*: whole brain analysis reveals cortical regions showing increased BOLD signal for rewarded minus nonrewarded trials, during the (auditory) feedback phase of the trial. Activations are projected onto axial, coronal, and axial MRI slices of a T1-weighted canonical brain, thresholded at $P < 0.005$ uncorrected for display. See RESULTS for coordinates, P values, and t scores. *B*: in visual ROIs, the difference in percent signal change between rewarded minus nonrewarded trials is shown, divided by the sum of activation for the ROIs in V1–V3 and for higher visual cortex (as identified on whole brain analysis). Normalized values are displayed to enable comparison between activity in these different visual areas, but all statistics were performed on actual percentage signal change. Error bars are SE of the difference between paired conditions. *C*: cortical regions showing increased BOLD signal for rewarded vs. nonrewarded trials during the feedback phase of the trial (threshold: $P <$ 0.005 uncorrected) shown in yellow, along with the combined ROIs for the gratings in V1–V3 for 11 participants (shown in blue), all projected onto coronal, sagittal, and axial MRI slices of a T1-weighted canonical brain at the coordinates shown. Note that the regions responding to rewarded trials are anterior and lateral to the ROIs in V1–3.

contralateral versus ipsilateral attention [V1: $F(1,10) = 0.01$, $P = 0.90$; V2: $F(1,10) = 1.8$, $P = 0.21$] nor interactions between reward and attention for the ROIs in V1 and V2 [V1: $F(1,10) = 1.06$, $P = 0.33$; V2: $F(1,10) = 0.05$, $P = 0.83$], at this feedback stage of each trial. Intriguingly, for the ROI in V3, there was a main effect of attending to the contralateral side during the feedback period [$F(1,10) = 9.9$, $P = 0.01$] and an interaction between reward and side attended [$F(1,10) = 13.4$, $P = 0.004$].

The main effect of attention seen in V3 and not in V1 or V2 may be due to a relative lack of power or because the effects of attention are more evident in higher visual regions. The interaction between reward and attention in V3 is particularly intriguing as it suggests some lateralized effect of reward feedback following correct discrimination in the earlier retinotopic region of V3, which was not seen in higher visual areas or on whole brain analysis (see following text) and may suggest a distinct response to reward feedback in this visual area.

In contrast to the lack of effects from rewarding feedback (vs. no reward) on retinotopic cortex after correct versus incorrect discriminations, whole brain analysis revealed many more areas responding differentially to reward (vs. no reward) after correct versus incorrect discrimination. Importantly, we found bilateral activation of higher visual areas beyond retinotopic cortex (coordinates [28, −88, 8], $t = 5.41$, $P = 0.005$ and [−30, −88, 6], $t = 4.35$, $P = 0.046$, small volume corrected; see Fig. 3). The visual areas activated by this contrast (rewarded vs. unrewarded trials during nonvisual feedback, after correct vs. incorrect discriminations) were lateral and anterior to the ROIs in V1–V3 (see Fig. 3*C*). The peak coordinates ([−30, −88, 6] and [28, −88, 8]) fell within the range of area LO1, a region of the lateral occipital complex that shows robust orientation-selective adaptation to gratings defined by luminance, contrast, and orientation cues (Larsson and Heeger 2006; Larsson et al. 2006). It seems likely that the regions activated here during the feedback period of rewarded trials, after correct discrimination, are close to or within part of the lateral occipital complex.

In addition to these visual areas anterior to V1–V3, we also identified significant activation for rewarded trials (vs. unrewarded trials) at the feedback phase, following correct versus incorrect discrimination, in left ventral striatum (coordinates [−6, 14, −2], $t = 4.09$, $P = 0.049$ and [16, 16, 4], $t = 4.04$, $P = 0.099$ small volume corrected; see Fig. 3*A*). This area has previously associated with reward and reward prediction (Elliott et al. 2000; Knutson et al. 2001; O'Doherty et al. 2001). Differential reward-related activation was also detected in orbitofrontal cortex (OFC) (coordinates [−8, 38, −16], $t = 8.06$ $P = 0.067$, fwe corrected on whole brain analysis). A full list of areas activated by the contrast of reward (vs. no reward) at the feedback phase, following correct versus incorrect discrimination, is given in Table 1.

Finally we examined whether there were any effects of reward magnitude (high vs. low reward) at the feedback phase in either retinotopic cortex or on whole brain analysis. We found no significant (all $P > 0.6$ differential activation for this contrast in retinotopic ROIs. On whole brain analysis, significant activation was identified only in left precuneus (coordinates [−14, −46, 34], $t = 6.52$, $P < .005$ fwe-corrected), in the left substantia nigra (coordinates [−10, −20, −16], $t = 5.59$, $P = 0.001$ fwe-corrected) and left medial frontal gyrus (coordinates [0, 40, 42], $t = 3.86$ $P = 0.017$ fwe-corrected).

Several aspects of the results presented thus far reveal new phenomena that cannot be reduced to previously observed phenomena given the nature of our design. Unlike other studies (e.g., Serences 2008), here we dissociated rewarding feedback after correct performance from the time of visual stimulus presentation. Moreover we found no difference between correct and incorrect trials for the discrimination phase when participants viewed the gratings and the standard effects of contralateral attention were observed. Thus the differences we observed later during the feedback phase did not simply reflect carry over from equivalent effects present during the visual stimuli due to standard spatial attention then or due to higher nonspecific alertness on correct trials than incorrect. It was only during the later phase of receiving rewarding feedback after correct performance that critical new effects were observed in bilateral visual cortex beyond retinotopic areas (see Fig. 3). Note once again that the rewarding feedback at this point was only given auditorily with participants merely fixating an unchanging point on an otherwise uniform gray screen, yet bilateral visual cortex (beyond retinotopic areas) was systematically affected then.

Taken together, these data show that in the reward phase of the trial, the most prominent effects of reward (vs. no reward) were observed in bilateral retinotopic visual cortex immediately anterior to V1–V3 (consistent with the putative anatomical location of LO1), plus areas of striatum and prefrontal cortex previously implicated in reward processing, as well a lateralized effect seen in V3.

TRIAL-TO-TRIAL EFFECTS. Finally, we considered how receiving a reward on a given trial might affect brain activity on a subsequent trial (Pleger et al. 2008, 2009), given our behav-

TABLE 1. *Reward minus no reward during (auditory) feedback phase*

Location	Coordinates [*x, y, z*] (MNI space) of Peak Voxel	No. of Voxels in Cluster	T Value	*P* Value
Orbitofrontal cortex	−8, 38, −16	461	8.06	.067
Ventral striatum				
left	−6, 14, −2	112	4.09	.015*
right	16, 16, 4	61	4.04	.033*
Right putamen	32, −10, 4	786	6.74	.005
Left middle frontal gyrus	−22, 14, 62	681	5.63	.012
Left superior parietal lobe	−28, −68, 48	573	5.13	.027
Right visual region	28, −88, 8	524	5.41	.005*
Left visual region	−30, −88, 6	286	4.35	.046*

*Small volume corrected (see METHODS). MNI, Montreal Neurological Institute.

ioral findings in the preceding text that reward improved discrimination accuracy on a subsequent trial. We were able to link the trial-to-trial impact of receiving reward to BOLD activity in visual cortex during the visual-discrimination-phase for the *next* trial (cf. Pleger et al. 2008; for a somatosensory analogue). In retinotopic visual cortex, our ROI analysis revealed a significant interaction between the direction of attention (contra- vs. ipsilateral) in the discrimination phase of a trial and whether the *previous* trial had been rewarded (or not) in V1 [$F(1,10) = 5.42$, $P = 0.042$]. Paired *t*-test confirmed that this interaction was driven by higher responses for contralateral compared with ipsilateral attention in the discrimination-phase of trials immediately following receipt of a reward for the prior trial [$t(1,10) = 2.3$, $P = 0.043$] with no such effect following a nonrewarded trial [$t(1,10) = 1.075$, $P = 0.31$, NS]. Figure 4*B* plots the activity evoked in each condition). We did not find similar interactions in V2 [$F(1,10) = 0.80$, $P = 0.39$] nor V3 [$F(1,10) = 0.02$, $P = 0.9$]. Similarly, on whole brain analysis, there were no further significant clusters of activation for this interaction of preceding rewarded trials with attended side. The effect of reward (vs. no reward) from the preceding trial on the discrimination-phase of the next trial for V1 was not seen in V1 (nor any other area) for the feedback phase of the next trial. This suggests that reward administration on the previous trial affects subsequent BOLD responses of retinotopic areas to visual stimuli specifically at the previously rewarded location rather than resulting in more general feedback-related activity to retinotopic visual areas. This argues against accounts of our findings in terms of general resetting signals related to trial end (Jack et al. 2006) or nonspecific carry-over effects from the reward phase of previous trials, which would not be spatially specific as we find. Please note that as attended side was kept constant within each block, the previously-rewarded location was always the same as the discriminated location at the subsequent trial. Future variants of our design could explicitly examine whether the trial-by-trial reward-feedback effects on BOLD signal and performance are retinotopically specific by varying the location of visual stimuli in a trial-by-trial fashion.

Taken together, our data show that receiving reward was associated with improved performance on the subsequent trial (but not across larger clusters of trials, see *Behavioral data*) and also with significantly enhanced activity on that subsequent trial for stimulus-specific representations in primary visual cortex on the attended side.

Eye tracking analysis

Long-range infra-red eye tracking confirmed there were no significant differences (all $P > 0.3$) between different trial types in mean eye position in the horizontal direction (our stimuli were arranged horizontally) neither in the discrimination phase nor the reward phase of the trial. Likewise there were no significant differences (all $P > 0.2$) in the SD of eye-position between trials types, contrary to expectations if saccades had occurred systematically in some conditions more than others.

Pupil size was slightly but significantly larger during unrewarded compared with rewarded trials at the point of feedback [2.1% larger in the unrewarded trials, $F(1,5) = 7.5$, $P = 0.04$]. Note that this difference cannot plausibly account for the changes in BOLD signals we observed during the feedback phase, which were in the opposite direction [i.e., greater BOLD signal on rewarded versus unrewarded trials at the feedback phase in bilateral visual cortex beyond retinotopic areas (Fig. 3); while the pupil size differences we observed should if anything result in slightly *less* retinal illumination on rewarded vs. unrewarded trials].

DISCUSSION

Here we dissociated brain activity associated with visual discrimination when attending to one or other hemifield from brain activity associated with subsequent (nonvisual) receipt of rewarding feedback after correct or incorrect visual discrimination, as signaled auditorily. We also examined trial-to-trial effects whereby rewarding feedback on one trial influenced performance and brain activity on the next trial. We found that BOLD signal in parts of visual cortex was modulated for all three of these successive points but that the anatomical locus and nature of these modulations differed.

During visual discrimination (before reward delivery), activity in retinotopic ROIs representing the visual gratings was modulated by spatial attention as expected, in accord with many previous findings that retinotopic cortex can be modulated by spatial attention during task performance. For retinotopic areas, anticipation of high (vs. low) reward modulated activity only in V2 (with a trend in V3); whereas higher visual areas (anterior to retinotopic areas V1–V3) showed no effects of reward level during the visual-discrimination phase (when attentional effort associated with reward incentive might conceivably have arisen but did not affect those areas). Furthermore there were no effects of correct versus incorrect discrimination in any visual areas during visual discrimination, suggesting that the subsequent effects of reward receipt following a correct discrimination (see following text) do not merely reflect some carry-over of differences in signal actually arising during discrimination. Here we were able to dissociate the discrimination and feedback phases.

As the trial progressed, auditory feedback signaled reward (or no reward) following correct or incorrect visual discriminations, respectively, at a time when no visual stimuli were present (unlike some other recent observations of reward/value modulations of visual processing) (Krawczyk et al. 2007; Serences 2008; Small et al. 2005). Despite the auditory nature of our feedback, we nevertheless observed significant activity increases in higher visual cortex (beyond retinotopic cortex) when reward versus nonreward was signaled following correct or incorrect discriminations. These signals in higher visual areas reflected a categorical effect of reward versus nonreward feedback (after correct or incorrect discriminations, respectively) rather than just trial end or resetting (Jack et al. 2006) as the latter should affect rewarded/correct and nonrewarded/incorrect trials equally at trials end. Our feedback signals were also associated with activity in ventral striatum and OFC, well known to be activated by reward (Elliott et al. 2000; Knutson et al. 2001; O'Doherty et al. 2001).

The higher visual areas activated by rewarding versus nonreward feedback, after correct versus incorrect discrimination, were anterior and lateral to retinotopic V3 (Fig. 3), overlapping with coordinates identified previously as part of the lateral occipital complex (Larsson and Heeger 2006). This area is sensitive to the orientation of gratings (Larsson et al. 2006)

similar to those used in the current study, but its responses are not strongly lateralized with respect to field of presentation. Our observation of feedback-associated activation of this area may therefore be consistent with an impact on neural representations of oriented stimuli at this intermediate level of visual processing. In contrast, we did not find any differential effect of feedback on earlier (lateralized) retinotopic representations in areas V1 and V2 that are known to contain neural populations selective for stimulus orientation (Hubel and Wiesel 1968; Kamitani and Tong 2005), although we did find a lateralized effect of reward in ROIs representing V3. Our data thus indicate both that feedback signals arising after discrimination can modulate higher visual cortex even in the absence of visual stimulation and that the effects on neural populations representing a stimulus differ qualitatively at different levels of the visual system (with feedback effects being found in nonretinotopic visual regions here).

It might be suggested that the effects that we observed in higher visual cortex during rewarding feedback might reflect some other process than the reward itself despite its timing. For example one might posit greater arousal or attention during trials that turn out to correct and hence subsequently get rewarded. But explanations of this type, relating to the correctness of the discrimination itself, should presumably lead to greater effects during the discrimination itself rather than at the later temporally decorrelated feedback stage. Yet the effects on bilateral nonretinotopic visual cortex (Fig. 3) were found at the latter point. It is this separation of the discrimination phase from the subsequent rewarding-feedback phase that allowed our study to uncover new phenomena.

Recall that the effects found for the feedback-phase arise for a point in the trial with no visual stimulation only an auditory signal. Spatial attention is known to modulate activity in visual cortex related to preparation for, and processing of, task-relevant visual stimuli (Kastner and Pinsk 2004; Silver et al. 2007), as observed for V1–V3 during the discrimination-phase here (Fig. 2). But note that we did not manipulate spatial attention at the feedback stage nor did we observe spatial-attention-like effects in V1–V3 during that later stage (Fig. 3). One might suggest instead that the rewarding feedback might have been intrinsically more "arousing" than the nonreward feedback. But please note that here this contrast at the feedback-phase specifically revealed activation in classic reward-associated regions (OFC and ventral striatum), as well as regions of nonretinotopic visual cortex that have recently been implicated in visual-discrimination tasks (Larsson et al. 2006). Given our use of a visual-orientation task also, this indicates a more specific feedback effect than merely nonspecific arousal when rewarded. Moreover by separating the discrimination phase from the later feedback phase, our design controls for any nonspecific effects applying throughout the whole trial.

In our study, delivery of reward rather than nonreward was always associated with correct versus incorrect discriminations (as in most previous studies of reward influences on perception also) (Della and Chelazzi 2006; Leon and Shadlen 1999; Libera and Chelazzi 2009). Nevertheless we were still able to dissociate the discrimination phase from the rewarding feedback phase as explained in the preceding text. In this study, we did not endeavor to provide random rewards regardless of correctness as we wanted to incentivize correct performance and wished to avoid the oddball events if feedback were to occasionally become nonveridical. Nevertheless it might be interesting in future extensions of this work to include some trials where the reward received deviates from veridical expectations and thus might trigger reward-prediction errors (Schultz 2006). Mere expectation of reward is well known to activate reward pathways in cognitive tasks with probabilistic outcomes (e.g., Preuschoff et al. 2006; Rolls et al. 2008; Tobler et al. 2007).

Our findings provide new evidence that rewarding feedback can modulate specific regions of human visual cortex. This is potentially consistent with emerging studies exploring possible impacts of reward for mammalian visual cortex. For example, pairing a visual stimulus with subsequent reward leads to a proportion of neurons in rat primary visual cortex expressing activity that predicts reward timing (Shuler and Bear 2006). In humans, reward is associated with improved visual performance (Seitz et al. 2009), and visual cortex activity can be increased by reward expectation (Krawczyk et al. 2007; Small et al. 2005). However, unlike the present work, those recent studies did not dissociate a feedback phase from the visual discrimination itself and therefore did not demonstrate that nonvisual reward signals per se can evoke visual cortex activation as shown here.

Our work also differs fundamentally from previous work in non-human primates showing that neurons in parietal cortex represent the value of competing choices (Platt and Glimcher 1999; Sugrue et al. 2004) and a recent fMRI study in humans showing value-based modulation as early in the visual processing pathway as V1 (Serences 2008). Those studies characterized the effects of value tied in a sustained manner to a particular stimulus or region of space, whereas in our study, we examined the effects of rewarding feedback after each trial (analogous to Pleger et al. 2008 in the somatosensory domain). Our study design also allowed us to examine the effects that rewarding feedback might have on discrimination ability and brain activity for the very next trial (see following text).

The effect of nonvisual rewarding feedback on (higher) visual cortex found here (Fig. 3) might potentially reflect a "teaching signal," possibly propagated via feedback connections from areas involved directly in reward processing and involving neuromodulators such as dopamine (see Pleger et al. 2009) and/or noradrenaline. Future studies might test such possibilities, using effective connectivity analysis in conjunction with pharmacological manipulations. Dopamine is released following stimuli that predict reward (Romo and Schultz 1990), and noradrenergic neurons may respond to unpredicted more than predicted rewards (Aston-Jones et al. 1994; Foote et al. 1980). Although dopaminergic innervation of the visual cortex is relatively sparse (Berger et al. 1988), even primate visual cortices receive at least some dopaminergic fibers (Berger and Gaspar 1994). Feedback messages carried by dopamine and/or noradrenergic neurons might influence the efficacy of synaptic transmission, providing a potential mechanism for how behavioral learning via reward feedback (Schultz and Dickinson 2000) may result in improved visual perception via enhanced sensitivity to relevant stimulus features (Seitz et al. 2009).

The direction of spatial attention to our lateralized gratings modulated retinotopic activity during discrimination, but we found no evidence for lateralized modulation by rewarding feedback in V1 or V2 at the feedback phase (which instead was associated with bilateral modulation of higher visual areas, plus an intriguing interaction in V3). What mechanisms could explain

how reward signals delivered to higher visual areas might subsequently influence neural activity associated with task performance in a lateralized discrimination? One possibility is that the neuronal representations modulated in higher visual cortex have some critical role in task performance (potentially consistent with their role in representing orientation) (see Larsson et al. 2006). But our data also provide tentative support for a further mechanism. Specifically, our trial-to-trial analyses revealed that receiving reward on the preceding trial was associated with improved accuracy for the visual discrimination on the *subsequent* trial, indicating a trial-to-trial behavioral effect of reward. This effect applied to successive pairs of trials rather than extending over longer clusters (see Fig. 4*A*), ruling out the possibility of slow fluctuations in nonspecific factors such as arousal. The fMRI data revealed that during the visual-discrimination phase of the very next trial after receipt of rewarding feedback, there was enhanced BOLD signal associated with the stimulus representation in primary visual cortex contralateral to the currently attended grating (see Fig. 4*B*). This indicates that receiving a reward at the end of one trial (which affects higher visual cortex) was associated not only with more accurate visual discrimination on the next trial but also with enhanced signals in lateralized early retinotopic cortex representing the task-relevant stimulus during the discrimination phase of the next trial. Thus the reward signals we observed in higher visual areas during the reward phase of a trial may lead to interplay between those higher visual areas and lateralized stimulus representations in earlier visual cortex that process the task-relevant stimulus on a subsequent trial. One potential interpretation of this is that receiving rewarding feedback on one trial may then lead to enhanced spatial attention during the discrimination-phase of the next trial. Such an account remains possible rather than proven but might be tested in future variations of our paradigm (e.g., by manipulating whether or not subjects know which side to attend to on the next trial following rewarding feedback).

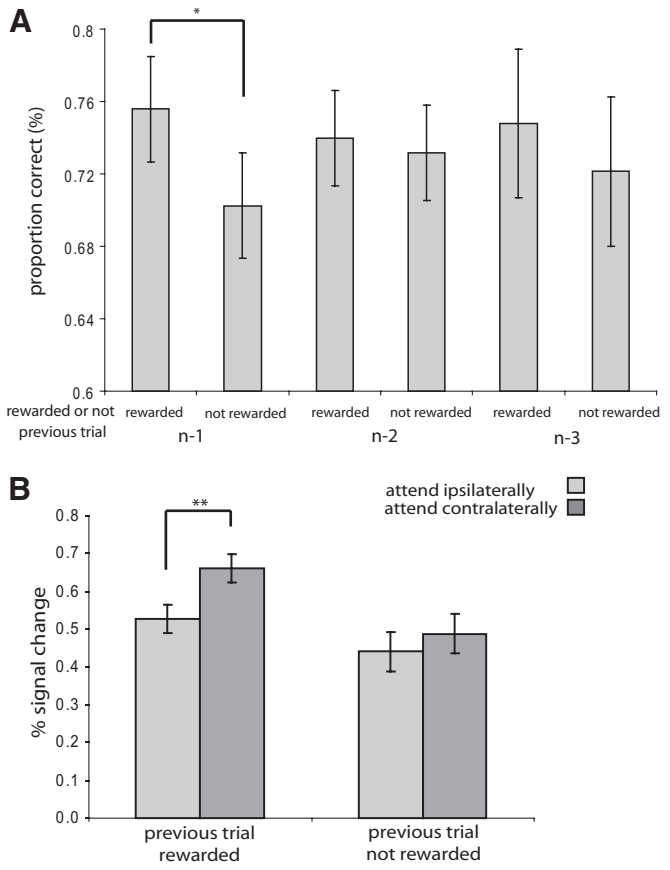

FIG. 4. Trial-to-trial effects of receiving reward feedback following correct discrimination. *A*: behavioral results. Receiving reward feedback on the previous trial ($n - 1$) was associated with improved accuracy on the *subsequent* trial, compared with after a trial that had not been rewarded. However, this effect was not seen for earlier trials: there was no improved accuracy on trials where the previous but 1 trial ($n - 2$) was rewarded or where the trial prior to that had been rewarded ($n - 3$). Group means of 12 participants are shown. Error bars indicate the SE of the difference between paired conditions; *, statistical significance. ($P = 0.05$, 1-tailed paired *t*-test). *B*: effect of trials receiving reward feedback on percent signal change in V1. BOLD signal change (percent relative to the global mean) averaged across 11 retinotopically mapped participants, for the V1 stimulus-responsive ROI, during the visual-discrimination phase of the trial, shown for trials subsequent to reward feedback, or to nonreward feedback, separately when attending to ipsilateral or contralateral gratings. Note that for trials preceded by reward feedback, there is a greater difference in percent signal change between attending to a contra- vs. ipsilateral grating, than after unrewarded trials. Error bars indicate the SE of the difference between paired conditions; **, statistical significance ($P < 0.05$, 2-tailed paired *t*-test).

The effects of monetary reward on visual selective attention have recently been explored behaviorally. Della Libera and Chelazzi (Della and Chelazzi 2006; see also Libera and Chelazzi 2009) reported a differential effect of reward on negative priming in a task with reward feedback. Specifically, distractors had a stronger subsequent effect on a visual task when associated with high rather than low financial reward.

Our work may be compared with the effects of rewarding feedback on somatosensory cortex (Pleger et al. 2008, 2009). While those studies show lateralized reactivation of primary somatosensory cortex during reward feedback, our study shows bilateral activation of higher visual areas with effects contralateral to the stimulus only for the subsequent trial. Importantly, the overall sample size was identical between these studies, making differences in power associated with sample size an unlikely explanation for the differences in findings. Instead it seems possible that the differences between these studies reflect differences in the architecture by which reward signals affect different sensory cortices (possibly due to anatomical proximity of somatosensory cortex to reward areas, different levels of dopaminergic innervation, and/or a more hierarchical organization of processing in visual cortex). Alternatively, the differences may reflect the specific task and stimuli in each experiment. Although we sought to optimize our task here for evoking primary visual cortex responses, it is possible that discriminating the orientations of two gratings presented sequentially over a delay requires input from higher visual areas (Larsson et al. 2006). Learning might also be more involved in the current study than for the somatosensory stimuli used in (Pleger et al. 2008) because of larger numbers of possible combinations of gratings in our task (8 possible gratings in our task, compared with four frequency combinations in the somatosensory study). Finally, the somatosensory studies found effects of reward magnitude on signals in human primary somatosensory cortex when they used four different levels of reward, whereas here for simplicity we used only two levels. Despite these differences, there are many similarities between the somatosensory studies of Pleger and colleagues (2008, 2009) and our current findings. These include: responses of ventral striatum and orbitofrontal cortex to reward, clear findings that sensory cortices (whether somatosensory or

visual) can be affected by rewarding feedback, and presence of trial-to-trial effects, whereby receipt of reward on one trial leads to an enhanced response in contralateral primary cortex for the discrimination-phase of the next trial as well as to better performance.

Conclusion

Here we demonstrated effects of rewarding feedback on higher visual areas (beyond retinotopic cortex), when this feedback was presented after correct visual discrimination but in the absence of current visual stimulation. We also found effects of this feedback on the next trial. Specifically, there was improved behavioral performance and increased activity in human primary visual cortex during the discrimination period subsequent to rewarding feedback. We thus provide new evidence consistent with a teaching signal being propagated (possibly from ventral striatum and/or orbitofrontal cortex) to higher visual areas, and ultimately impacting on primary visual cortex contralateral to the location of a visual target during discrimination at the next trial after feedback. Having documented such influences, further work is now needed to characterize whether these influences may be task-dependent or reflect a more general architecture for how rewarding feedback after correct discriminations can influence visual processing.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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