Current Biology *18*, 419–424, March 25, 2008 ©2008 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2008.02.047

Report

Neural Correlates of Social Target Value in Macaque Parietal Cortex

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Summary

Animals as diverse as arthropods [1], fish [2], reptiles [3], birds [4], and mammals, including primates [5], depend on visually acquired information about conspecifics for survival and reproduction. For example, mate localization often relies on vision [6], and visual cues frequently advertise sexual receptivity or phenotypic quality [5]. Moreover, recognizing previously encountered competitors or individuals with preestablished territories [7] or dominance status [1, 5] can eliminate the need for confrontation and the associated energetic expense and risk for injury. Furthermore, primates, including humans, tend to look toward conspecifics and objects of their attention [8, 9], and male monkeys will forego juice rewards to view images of high-ranking males and female genitalia [10]. Despite these observations, we know little about how the brain evaluates social information or uses this appraisal to guide behavior. Here, we show that neurons in the primate lateral intraparietal area (LIP), a cortical area previously linked to attention and saccade planning [11, 12], signal the value of social information when this assessment influences orienting decisions. In contrast, social expectations had no impact on LIP neuron activity when monkeys were not required to make a choice. These results demonstrate for the first time that parietal cortex carries abstract, modality-independent target value signals that inform the choice of where to look.

Results and Discussion

Neurons in lateral intraparietal area (LIP), as well as other areas including the prefrontal cortex [13], posterior cingulate cortex [14], and superior colliculus [15], signal the value of fluid rewards expected for orienting to a visual target. Such reward modulation is commonly interpreted as a mechanism that biases the visual orienting system to shift gaze, and possibly covert attention [16], to the most important among potential targets. Despite the attractiveness of this idea, it is difficult to imagine a natural situation in which a saccade would be rewarded immediately with a drop of juice. Moreover, simply training monkeys to make eye movements in response to visual and auditory stimuli for fluid rewards alters neural activity in LIP [17, 18] and other cortical areas [19]. These observations raise the possibility that reward-related modulations in LIP, as well as other areas, observed in previous studies may have reflected, at least in part, changes in neuronal responses related to the use of fluid rewards to motivate conditioned orienting behavior rather than the intrinsic, adaptive value of looking at a particular object in the visual scene.

To address these issues, we probed whether the value of visual information provided by looking at a particular target modulates parietal neuron activity in the same way that fluid rewards do. Given the importance of visual social cues to primates [5, 10], we hypothesized that neural activity in LIP would reflect the value of visually acquired social information. To test this hypothesis, we recorded responses of LIP neurons while monkeys performed a visual choice task that permitted us to quantify the value monkeys place on different classes of visual information [10].

In each choice trial, two adult male rhesus macaques (*Macacca mulatta*) chose between two targets with a gaze shift. Choosing one target (T1) delivered juice (measured in ms of open solenoid time, see Experimental Procedures and [20]); choosing the other target (T2) delivered juice and the display of an image (Figure 1A). Images were drawn from pools of photographs of the faces of familiar male monkeys, the hindquarters of females, and a gray square. The substitutability of social and fluid rewards was estimated by varying the amount of fluid delivered for T1 and T2 choices across blocks of trials—a variation on the method of constant stimuli [21]—and then calculating the point of subjective equivalence (PSE) (Figures 1B and 1C, see also Experimental Procedures and [10]). The sign-inverted PSE served as our measure of image value: Positive values indicate image sets monkeys would forego fluid to see, whereas negative values indicate image sets monkeys required fluid overpayment to view.

Consistent with previous results [10], monkeys differentially valued images of other monkeys based on social status and reproductive salience (Figure 1D). Specifically, when data from both subjects were collapsed, monkeys significantly preferred female hindquarters (13.8 ± 2.7 ms [SEM], two-tailed t test against 0, $p < 10^{-4}$, n = 31 image blocks), showed a significant aversion to subordinate monkeys (−13.0 ± 4.4 ms, $p < 0.01$, n = 20), were indifferent to the gray square (1.7 ± 2.2 ms, $p = 0.45$, n = 44), and showed a trend toward valuing dominant monkeys (6.5 ± 3.4 ms, $p = 0.07$, n = 25). Although preferences for faces of dominant males did not achieve significance when tested against neutrality (image value = 0), they were preferred to subordinates (two-tailed t test, $p < 0.005$), indicating differential preferences for male faces based on status.

Our published data indicate that once male monkeys choose to look at an image, they continue to view female hindquarters

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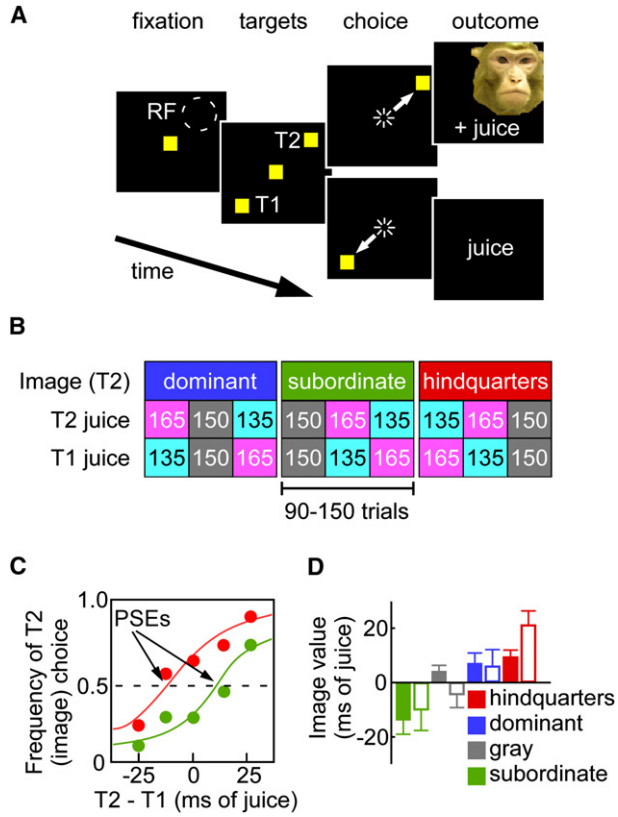

Figure 1. Task Setup and Behavioral Data Analysis

(A) Choice task. The monkey first fixates a central square (300–450 ms). Next, two peripheral response targets (T1 and T2) appear. T2 always appeared in the response field (RF) of the neuron being recorded; T1 appeared directly opposite T2. After a second delay (300–500 ms), the central square disappeared, and the monkey was free to shift gaze to either T1 or T2. If he chose T2, he was rewarded with juice and an image was displayed for 500 ms (image not shown to scale); T1 choices were rewarded only with juice. Single-target trials were identical except that only one target appeared and only gaze shifts to that target were rewarded.

(B) Example block design. Three to five smaller blocks of varying fluid values (30–50 trials) comprised each larger image block (90–150 trials).

(C) Estimating social image value. For each pool of images, the frequency of choosing T2 was plotted against the difference in fluid rewards (T2 − T1, measured in ms of open valve time). These data were fit with a cumulative normal function. The point on the abscissa where this function crossed 0.5 on the ordinate was taken as the PSE. The sign-reversed PSE served as our measure of image value. Example psychometric functions derived from a single session for hindquarter (red) and subordinate face (green) image blocks.

(D) Monkeys differentially valued different classes of images (one-way ANOVA, main effect of image class: Monkey S (closed bars), ($F_{(3, 72)} = 8.0$, $p < 0.001$); Monkey D (open bars), ($F_{(3, 40)} = 5.5$, $p < 0.005$). Error bars represent SEM.

longer than they do the faces of dominant or subordinate males [10], and these findings were replicated here (Figure S1 available online). We interpret this to indicate that male macaques value the opportunity to see female hindquarters and the faces of dominant males because they predict potential reward and threat, respectively (cf. [10]). These data indicate that monkeys choose to look at stimuli that carry valuable social information for guiding behavior, independent of their hedonic properties.

LIP neurons also were sensitive to the value of images displayed for orienting to targets in their response fields (RFs). Figure 2A shows the average activity of an example LIP neuron for all trials in which T2 was in the RF and the monkey chose to look at it, plotted as a function of image class but unsorted with regard to fluid outcome. Firing rate clearly mirrored the monkey's behavioral preferences for different classes of images. Figure 2B quantifies this relationship by showing the average firing rates for each image class for four 200 ms epochs measured on these trials. The activity of this neuron was modulated by fluid value in a similar fashion (Figures 2C and 2D) when the data were collapsed across image classes.

Population-level analyses yielded the same result. We selected neurons on the basis of possessing a spatially specific increase in activity after target or saccade onset in a delayed saccade task used to map the RF of each neuron encountered. Consistent with prior studies [22, 23], about 40% of neurons (34/82) met this criterion. By using two-way ANOVA, we next analyzed the activity of these 34 neurons (15 from monkey D and 19 from monkey S) during trials in which the monkey chose to look at T2. We predicted that if LIP neurons encode the independent contributions of social image value and fluid value to the decision to orient to a particular target, then this analysis would reveal main effects of each variable but no interaction. Figure 3A shows firing rates for each epoch separated into bins of high, medium, and low fluid and image value (see the Experimental Procedures). A two-way ANOVA revealed a significant ($p < 0.001$) main effect of image value on firing for every epoch, as well as a main effect of fluid value ($p < 0.005$) for the posttarget and presaccade epochs but no interaction between the two factors for any epoch ($p > 0.33$). Thus, LIP neurons appeared to encode the integrated value of orienting to a particular target, derived from both fluid and social outcomes.

Next, we plotted average firing rate as a function of time segregated by image class and collapsed across all juice-reward sizes (Figure 3B; for a corresponding plot segregated by fluid value see Figure S2). Firing rate increased with both increasing image preference and increasing fluid rewards. Linear regression of firing rates against image value revealed significant positive correlations for all epochs (Figure 3C, black symbols). When the effect of fluid value on average neural response was examined, a similar relationship was observed (Figure 3D, black symbols). The same regressions also were performed on a data set restricted to trials in which the fluid payoffs for orienting to T1 and T2 were equal (Figure 3C, gray symbols). Similarly, Figure 3D (gray symbols) shows the effect of fluid outcome on firing rates for the data set restricted to image blocks in which image value was neutral (±5 ms). Even in these restricted cases, the LIP population response encoded both the social value and the fluid value of a visual target. We also performed a multiple regression analysis on the firing rates of each neuron by using image value, fluid value, saccade latency, amplitude, and peak velocity as independent variables. By this analysis, the firing rates of 44% of our neurons were significantly positively correlated with image value in one or more epoch; 27% were positively correlated with fluid value. We interpret these results to demonstrate that LIP maintains an abstract representation of the expected value of orienting to a visual target independent of the modality or hedonic qualities of the expected outcomes. Social rewards, social threats, and the expectation of a large squirt of juice all evoked enhanced firing by neurons in LIP.

The above analyses were performed on choice trials. For the majority of cells (30/34), we also included randomly interspersed single-target trials (20%–40%) (see the Experimental Procedures). Figure 4A plots average activity for the population of 30 LIP neurons recorded with interspersed single-target trials with T2 as the target. In contrast with choice trials, there was

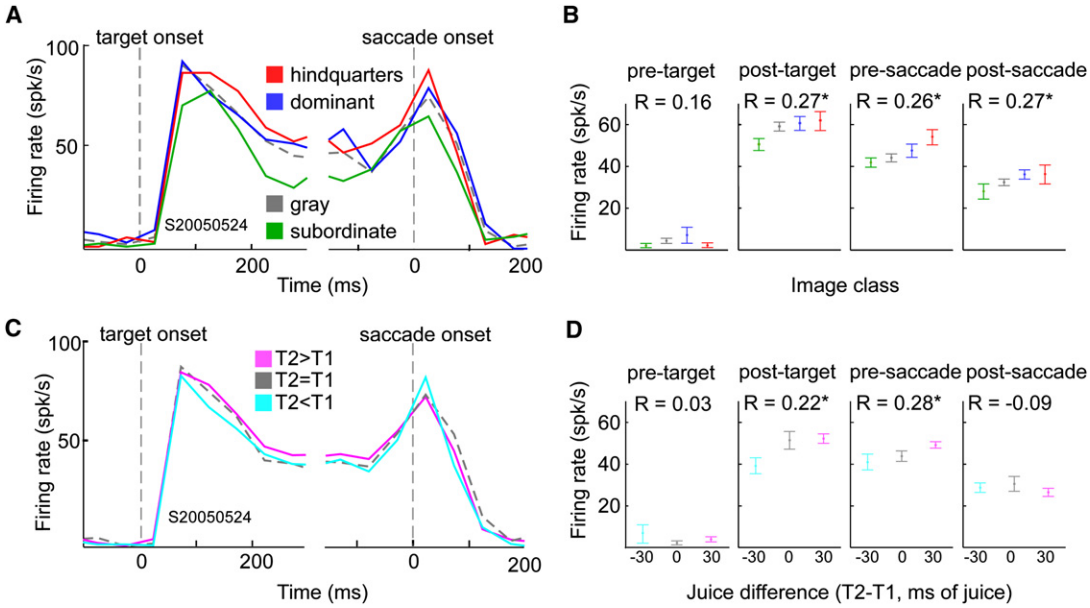

Figure 2. Single LIP Neurons Encode Social-Image Value and Fluid Value

(A) Average activity of a single LIP neuron separated by image class and averaged for all trials in which the subject chose T2, aligned on peripheral target onset (left) and saccade onset (right).

(B) Average firing rates (±SEM) plotted against image class for the same neuron in four 200 ms epochs on trials in which the subject chose T2 (Spearman rank R-values, n = 88 trials). Spearman rank order correlations were used because image values for this dataset were not normally distributed (Shapiro-Wilk's W = 0.73, $p < 0.01$). *$p < 0.02$.

(C) Same format as (A). Data are separated by difference in fluid payoff between T2 and T1.

(D) Same format as (B). Firing rates plotted as a function of the difference in fluid payoff between T2 and T1. *$p < 0.05$, also by Spearman rank correlation.

significantly less modulation by image value in single-target trials (ANCOVA: trial type × image value interaction, $p < 10^{-4}$ for every epoch). Our single-cell example showed the same effect (Figure S3).

These data invite the hypothesis that LIP neurons convey information about the relative and not absolute value of orienting to a target (cf. [24]; but see [16]), irrespective of whether value is computed on social or fluid expectations. The small modulation apparent in interspersed single-target trials presumably reflects the fact that the number of targets on a trial was unknown prior to target onset. To explore this idea, we tested a subset of neurons (n = 18; 9 in each monkey) in blocks made up exclusively of single-target trials (Experimental Procedures). Under these conditions, there was no modulation of firing rate by social-image value (Figure 4B). Similarly, modulation by juice value was abolished in both interspersed and blocked single-target trials (Figure S4). To directly illustrate the loss of modulation when a choice was not required, Figures 4C and 4D show the effects of image value on average neural response for the 11 neurons for which we were able to gather data on both choice trials and blocked single-target trials. Although the firings rates of this subset of neurons maintained a significant positive relationship to image value in choice trials, only the postsaccade epoch ($p = 0.04$) showed this relationship in blocked single-target trials. Together, these data corroborate previous findings that fluid-value modulation of LIP activity only occurs when there are two or more potential targets for saccades [12] and extends these findings to social-image value.

Conclusions

Our results demonstrate, for the first time, that neurons in LIP, a cortical brain area previously linked to visual attention [25], saccade planning [22, 26], and reward-guided oculomotor decision-making [11, 12], signal the value of social information when this assessment is used to guide orienting decisions. In contrast, social expectations had no impact on LIP activity when monkeys were instructed to make the same movement to view the same images. Importantly, LIP neurons reflected the summed behavioral value of orienting to a particular target, integrated from expected social rewards and threats as well as expected fluid rewards, associated with that choice. Together, these results suggest that LIP neurons signal the relative value of the panoply of rewards and threats associated with looking at different locations in the visual world.

Our results are not easily explained by other factors. Most importantly, LIP neurons do not reflect target value when there is no opportunity to choose where to look. Thus, increases in general motivation or arousal due to enhanced reward expectations cannot be invoked to explain value-based modulations of firing rate in LIP. Similarly, changes in saccade metrics that accompany changes in reward contingencies, such as increased velocity or amplitude or decreased latency, cannot explain value-based modulation in LIP. When these factors were included in a multiple-regression analysis, 44% of neurons were positively modulated by image value. The lack of reward-related modulation in LIP when only one target was available is consistent with the previous suggestion that LIP represents target value relative to the sum of the value of all other available targets [24].

Our data also indicate that LIP neurons convey information about overall target value rather than the specific hedonic qualities of the outcome expected from orienting. It seems reasonable to conclude that monkeys find looking at female hindquarters rewarding because they continue to fixate on them for longer than any other stimulus but actually find looking at high-ranking males threatening because they look away from them more quickly (Figure S1 and [10]). Despite this clear difference

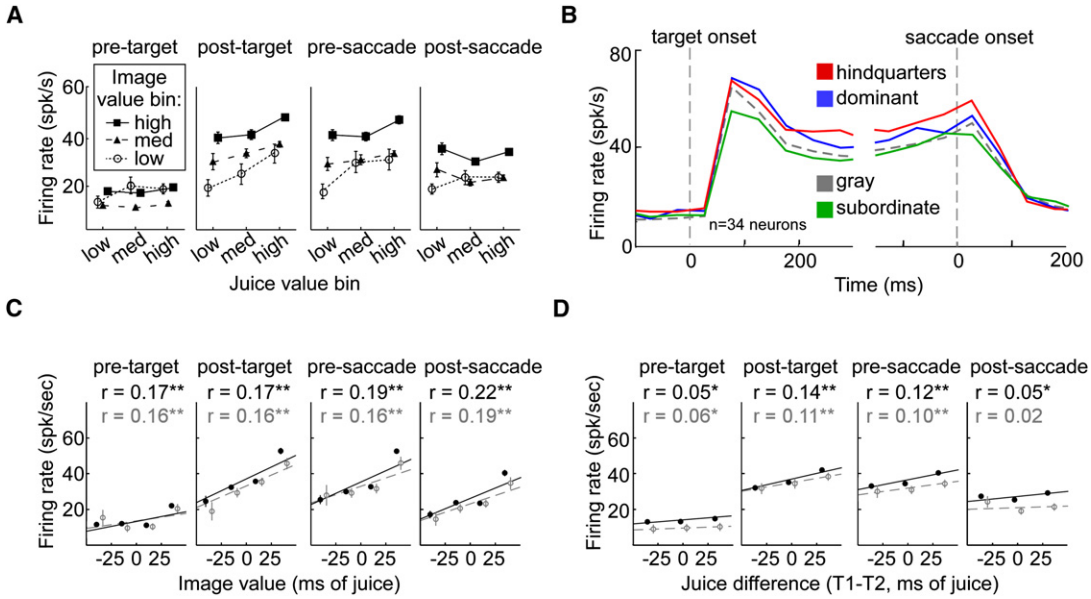

Figure 3. The LIP Population Response Simultaneously Reflects Image Value and Fluid Value during Target Choice

(A) Data from all trials in which the subject chose to view the image (T2) were placed into nine bins based on the fluid and image value of the trial. Two-way ANOVA revealed a main effect ($p < 0.001$) of image-value bin on firing rate for every epoch, juice-value bin on firing rate ($p < 0.005$) for posttarget and presaccade epochs, and no interaction ($p > 0.33$) for any epoch. Error bars represent SEM.

(B) Average firing rate for 34 neurons plotted against time for all trials in which the subject chose to view the image (T2) in the neuron's response field, separated by image class.

(C) Firing rates plotted as a function of image value in four 200 ms epochs. Data are binned for display, but regressions were performed on raw data. Black symbols represent regressions performed on all data in which the subject chose to view the image, and gray symbols represent the same analysis restricted to trials in which the fluid payoff for choosing T1 was equal to T2. Error bars represent SEM.

(D) Firing rates plotted as a function of the difference in fluid payoff between T2 and T1. Data are binned for display, but regressions were performed on raw data. Black symbols represent regressions performed on all data in which the subject choose view the image, and gray symbols represent the same analysis restricted to trials in which the image value calculated for that block was greater than −5 and less than 5 ms. *$p < 0.05$, **$p < 10^{-3}$. Error bars represent SEM.

in the hedonic properties of female hindquarters and high-ranking male faces, monkeys chose to look at both classes of stimuli at similar frequencies. These observations suggest that LIP has access to behaviorally relevant, but hedonically positive and negative, information associated with particular locations in the visual field.

We also note that LIP neurons would likely encode the value of any nonsocial, but behaviorally relevant, visual stimulus in a manner similar to that described here. Thus, LIP does not encode social value per se, but only the abstract value of orienting to a particular target. Nonetheless, LIP must incorporate the value of social information into this abstract representation. Given the importance of visual social information to primates (reviewed in [5]) and the social-rank-dependent viewing behaviors observed here (Figure 1D and Figure S1) and elsewhere [10, 27], we find it unlikely that nonsocial factors motivated the behavior observed in this and previous [10] studies.

Finally, our data demonstrate that the representation of target value in LIP is important for orienting decisions in natural contexts and not simply an artifact of experimental paradigms typically used to study neural function, in which eye movements are immediately rewarded with fluid. Our results also suggest that LIP reflects value-related information from social and nonsocial sources equivalently, a prerequisite for executing final orienting decisions in an environment with many diverse factors competing for attention. Determining the precise neuroanatomical source of the common currency of value, as well as how such a currency is computed and applied to target locations, constitutes an important goal for future studies.

Experimental Procedures

Subjects and Housing

Subjects were two adult male rhesus macaques (*Macaca mulatta*) housed in a colony of 10 males and 4 females. All males were pair housed, wherease females were cohoused. Dominant and subordinate statuses were determined relative to the cagemate by unidirectional submissive displays [10]. The dominance relationships of each pair were stable for at least a year before the beginning of the study and remained unchanged for the duration of the study. Our subjects consisted of one dominant (monkey S) and one subordinate (monkey D). All animals were originally reared in social groups. To maintain motivation, subjects' water access was restricted outside of the experimental session. All procedures were approved by the Duke University Institutional Animal Care and Use Committee and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals.

Surgical and Training Procedures

In an initial sterile surgical procedure, a head-restraint prosthesis and scleral search coil [28, 29] were implanted by using standard techniques described in detail elsewhere [30]. After a 6 week recovery period, animals were habituated to head restraint and trained to perform oculomotor tasks for fruit juice rewards. In a second sterile surgical procedure, a stainless steel recording chamber (Crist Instruments) was implanted over area LIP, 3 mm caudal and 12 mm lateral to the intersection of the midsagittal and interaural planes. The chamber was kept sterile with regular antibiotic washes and sealed with replaceable sterile caps (Crist Instruments). After all surgeries, animals received analgesics for 3 days and antibiotics for 10 days.

Behavioral Techniques

By using the scleral search coil technique [29], horizontal and vertical eye position were sampled at 500 Hz (Riverbend Instruments). Alternately, for a minority of the data (seven neurons from monkey D), eye position was sampled at 60 Hz by infrared camera (Arrington Research). Custom software

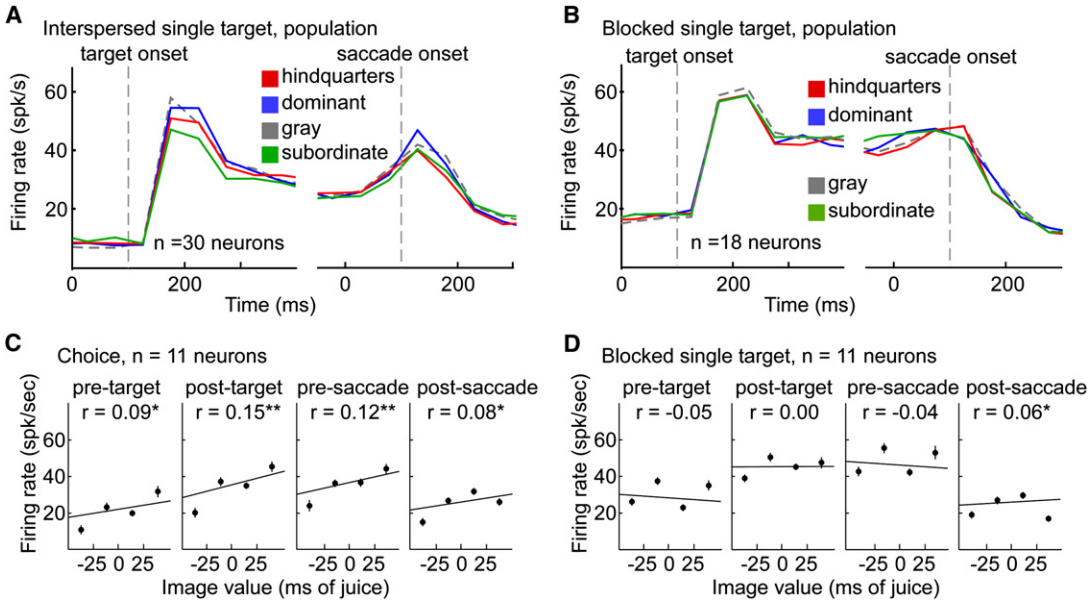

Figure 4. LIP Neurons Encode the Relative Value of Social Targets

(A) Firing rates on interspersed single-target trials for entire population of neurons studied with such trials (n = 30). Same format as Figure 3B.

(B) Firing rates of the entire population of neurons studied with blocks of single-target trials, for trials using T2. Same format as Figure 3B.

(C and D) Firing rates plotted as a function of image value for the 11 neurons tested in both choice trials (C) and single-target blocks (D). Data were binned for display, but regressions were performed on raw data. *p < 0.05, **p < 0.005. Error bars represent SEM.

(Ryklin Software) was used for recording eye position data, spike timing data, and visual stimuli presentation. Visual stimuli were presented over a dark background on a 24 inch CRT monitor (60 Hz refresh rate, 1024 × 768 resolution, placed 45 cm directly in front of the monkey).

A previously described choice task was used to examine the value of social images [10]. Trials began with a 500 Hz tone sounded for 300 ms immediately followed by the illumination of a centrally located yellow square (fixation onset). Subjects were required to fixate this target within 300 ms and maintain fixation (±5°). After a variable period of 300–450 ms, two peripherally located targets identical to the central target appeared. One target (T2) was located in the response field (RF) of the neuron being studied; the other target (T1) was located the same distance from the central target but directly opposite T2. After a 300–500 ms variable delay, the central target was extinguished, cuing the monkey to make a saccade to T1 or T2 and maintain fixation (±10°) for 500 ms. Upon completing the trial successfully, the monkey received a squirt of juice delivered through a tube connected to a solenoid; the amount of juice the monkey received was controlled by the duration of solenoid open time. When the monkey chose T2, he was rewarded with a juice squirt and the opportunity to view an image for 500 ms; when he chose T1 he received only juice. Juice delivery upon a successful saccade to either target was accompanied by a broadband noise burst of 300 ms duration. The amount of juice received for choosing each of the targets varied from 125 to 175 ms such that the average between the targets was always 150 ms. The volume of juice delivered was a linear function of open solenoid time [20] over the ranges used in this experiment, with 150 ms corresponding to 0.16 ml. Monkeys typically completed 1200–2200 trials per session.

Choice Blocks

We employed a nested block design in which three to five smaller blocks of constant juice values composed a larger image block in which all images viewed were drawn from the same image pool (Figure 1B). Juice blocks were 30–50 trials. Image blocks were typically 90–150 trials. The orders of image and juice blocks were varied pseudorandomly. We excluded the first five trials after any reward-contingency change from all analysis because image and fluid reward-contingency changes were not signaled.

In addition to the choice trials, single-target trials were randomly interspersed to promote target sampling. These trials were identical to the choice trials in terms of timing, target placement, juice rewards, and image presentation. In these trials only one peripheral target appeared and the monkey was only rewarded for shifting gaze to that target. Single-target trials made up 20%–40% of all trials for 30/34 neurons, and 0% for the remaining four neurons.

Single-Target Blocks

Some neurons (18, 9 neurons from each monkey) were tested in blocks made up entirely of single-target trials (50% T1 and 50% T2). These trials were identical to the single-target trials described above, but the block structure differed. Two types of blocks were used. In juice-varying blocks, the gray square was used as the image for 120–180 trials whereas juice delivered for each target varied symmetrically around 150 ms in a pseudorandom order, changing every 30–50 trials. In image-varying blocks, juice values were held constant at 150 ms for each target whereas the image category presented for a correct saccade to T2 varied in a pseudorandom order, changing every 30–50 trials. Typically, two juice- and two image-varying blocks were performed in pseudorandom order for each cell. The first five trials after any reward contingency change also were excluded from analysis in single-target blocks.

Stimuli

Images were produced from a 4.0 megapixel digital camera (Nikon CoolPix 4600). Twenty pictures from each of the familiar male monkeys composed each face image pool. Only images with a neutral facial expression were used. Each face image pool contained five to six images in which the monkey's gaze was directed at the camera; gaze was averted in the remaining images. The head was cropped from the background, and the image was resized to 115 × 115 pixels (5°). Mean luminance was adjusted to match the gray square (also 115 × 115 pixels). Two hindquarter pools each consisted of 20 images from all 4 females. Hindquarter images were normalized in the same manner as face images. In each image block, images were chosen from the corresponding image pool randomly with replacement.

Data also were collected from similar pictures of the faces of four familiar female monkeys. However, behavioral preferences and neural data for female faces were inconsistent from day to day. We believe this may be related to the position of the females in their estrus cycle at the time of the experiment. Although previous experiments [10] monitored the cycle position at the time the pictures were taken and found no effect, cycle position of the female monkeys at the time of the experiment may have affected behavioral preferences, as our subjects and female monkeys were housed in the same room. Unfortunately, we have no way to reconstruct this information; therefore, these data are not included in the discussion.

Recording Techniques

Electrophysiological recordings were conducted using standard techniques. Single electrodes were lowered until the waveform of a single neuron was isolated (BAK Electronics) and a computer recorded action potentials at 25 kHz. We identified LIP neurons by anatomical location and spatially specific visual or movement period activity in memory saccade trials [11, 22, 23, 31]. Neurons were recorded 8–12 mm lateral and 3–7 mm caudal to stereotaxic 0,0 and were located between 2 and 10 mm ventral to the cortical surface based on travel of the micropositioner. Delayed and memory saccade trials were used to select a position for T2 inside the neuron's response field.

Estimation of Image Value

The value of each image pool was estimated as described elsewhere [10]. Image value was derived from a cumulative normal function fit to relative juice payoff for choosing T2 plotted against the frequency of orienting to T2. The PSE was taken as the juice value at which the monkey would be indifferent between T1 and T2 (Figure 1). Sign-reversed PSEs were taken as image value. Image values were calculated for each image block. Image blocks in which the cumulative normal fit explained less than 25% of the variance in the choice data were excluded from analyses involving image values ($r^2 = 0.57 \pm 0.33$ SD for all image blocks, $r^2 = 0.70 \pm 0.23$ for surviving blocks). Thirty-six of 153 blocks were excluded based on this criterion. Image values were constrained to values between −40 and +40 ms. To correct for day-to-day variation in bias for a particular target location, normalized image values were created by subtracting a sign-reversed PSE created for all image blocks for that session from the image value for each image block. This normalized image value was used in all analyses. Behavioral data in the pay-per-view task has been previously collected from each monkey and published elsewhere. However, the data presented in Figure 1 and Figure S1 are unique to this study.

PSTHs were created from successful trials ending with gaze shift into the RF of the neuron being studied. For display, data for PSTHs were collapsed into 50 ms bins. For Figure 3A, data were placed into bins of high, medium, and low juice value based on the relative value of T2 (i.e., data from trials in which fluid reward for T2 was higher than T1 were placed in the high-juice-value bin). Data were divided into image-value bins such that the median of each bin was as close as possible to its corresponding juice bin. Statistical analyses were performed with Statistica 6.1.

Supplemental Data

Four figures are available at http://www.current-biology.com/cgi/content/full/18/6/419/DC1/.

Acknowledgments

We thank Dr. Ben Hayden, Stephen Shepherd, and Arwen Long for comments on the manuscript. Funded by EY013496 (M.L.P.), F31MH081443-01 (J.T.K.), and the Cure Autism Now Foundation (M.L.P.).

Received: November 30, 2007
Revised: January 30, 2008
Accepted: February 11, 2008
Published online: March 20, 2008

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