Neural correlates of decision variables in parietal cortex

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Decision theory proposes that humans and animals decide what to do in a given situation by assessing the relative value of each possible response. This assessment can be computed, in part, from the probability that each action will result in a gain and the magnitude of the gain expected. Here we show that the gain (or reward) a monkey can expect to realize from an eye-movement response modulates the activity of neurons in the lateral intraparietal area, an area of primate cortex that is thought to transform visual signals into eye-movement commands. We also show that the activity of these neurons is sensitive to the probability that a particular response will result in a gain. When animals can choose freely between two alternative responses, the choices subjects make and neuronal activation in this area are both correlated with the relative amount of gain that the animal can expect from each response. Our data indicate that a decision-theoretic model may provide a powerful new framework for studying the neural processes that intervene between sensation and action.

Neurobiologists have begun to focus increasingly on the study of sensory–motor processing, but many of the models used to describe these processes remain rooted in the classic reflex, initially described by Descartes[1] and later advocated by Sherrington[2] as a model system for studying the connection between sensation and movement. Sherrington, in particular, viewed response selection as a physical link between independent, anatomically distinct sensory and motor systems[2]. Until recently, the sensory–motor reflex was tacitly accepted by many physiologists as an appropriate model for describing the neural processes that underlie complex behaviour[3–5]. More recent findings indicate that, at least in some cases, the neural events that connect sensation and movement may involve processes other than classical reflexive mechanisms[6–9] and these data support theoretical approaches that have challenged reflex models directly[10–13]. Researchers outside physiology have long argued for richer models of the sensory–motor process[14–18]. These models invoke the explicit representation of a class of decision variables, which carry information about the environment, are extracted in advance of response selection, aid in the interpretation or processing of sensory data and are a prerequisite for rational decision making[19]. Here we describe a formal economic–mathematical approach for the physiological study of the sensory–motor process, or decision-making, in the lateral intra-parietal area (LIP) of the macaque brain.

Theoretical treatments of decision making

Although mathematical approaches to decision-making propose different formulae for identifying the response a subject should choose under a given set of conditions, nearly all theories require the decision-maker to have some knowledge of two environmental variables: the gain expected to result from an action and the probability that the expected gain will be realized. The expected value theory of Arnaud and Nichole[20], for example, proposes that a rational decision-maker should multiply expected gain by the probability of gain to establish an expected value for each course of action, and then should choose the option with the highest expected value. Although subsequent theorists have proposed different mathematical combinatorial rules that provide more accurate models of the decision-making process, knowledge of the gain expected from a response and the probability of realizing that gain is still considered to be critical to the computation of rational choice[19,20,22].

Ecological biologists[17,18] and psychologists[14–16] have also developed formal models of decision-making. Most of these models assume that animals make decisions that either maximize the rate of energy intake from different options or match their rates of behavioural responding to the reinforcement rates obtained from different choices. These models propose that animals choose on the basis of several variables, including the probability of reinforcement[23] and the magnitude of reinforcement[24,25] associated with different responses. Experimental evidence indicates that expected gain and probability of gain do influence the choices animals make.

However, neurobiological models of the processes that connect sensation and action almost never propose the explicit representation of decision variables by the nervous system. Most contemporary neurophysiological models, particularly models of cortical sensory–motor transformations, identify sensory and motor signals as critical components, but they rarely address the possibility that neural signals may encode data that fall outside these two categories. Our investigations have led us to propose that decision theory might provide a powerful alternative framework for studying the sensory–motor process. Our current model could be described as having two classes of inputs: current sensory data, and a stored representation of environmental contingencies. Current sensory data would reflect the observer's best estimate of the current state of the salient elements of the environment. As such, it would be influenced by stored information that could improve the efficiency of sensory processing through selective attention. The second class of inputs would represent the chooser's assumptions about current environmental contingencies, a class of inputs that detail how an action affects the chooser. Decision making would involve the combination of post-attentional sensory data with the subject's best estimate of the outcome of any given action. These estimates of environmental contingencies would then be combined with a loss function specifying the value of all possible losses and gains to the chooser, according to a decision rule like the one originally proposed by Arnauld and Nichole[20] or in subsequent refinements of their model[19,21,22].

Physiology of sensory–motor integration in LIP

Although neurobiologists have not employed decision-theoretic formulations of this type, many groups have concluded that a number of brain areas are involved in the processes that intervene between sensation and action. Parietal area LIP has been labelled attentional[26,27], decision-related[28] and motor-preparatory[29–31] by different groups. Our own work indicates that decision-theoretic models may provide a powerful alternative approach to the study of sensory–motor processing in parietal cortex[32,33].

In one study[34], we assumed that visual attention can be treated as conceptually separable from other elements of the decision-making process. We used two tasks that independently controlled both the location of a saccadic target and the location and behavioural relevance of a visual distractor. In both tasks, a monkey initially fixated a central stimulus, and then two eccentric stimuli were illuminated, one above and one below the central stimulus. A change in the colour of the central stimulus identified one eccentric stimulus as the eventual saccadic target and the other as a visual distractor. In one task, the distractor was highly relevant because offset of this stimulus signalled the animal to initiate a saccade to the target; in the second task the distractor was completely irrelevant, because offset of the central stimulus signalled the animal to initiate the saccade. Although intraparietal neurons were more active on blocks of trials in which a stimulus served as a saccadic target than on blocks of trials in which the same stimulus served as a visual distractor, none of the neuronal responses distinguished between behaviourally relevant and irrelevant distractors. We took this finding as preliminary evidence that activity in area LIP does not participate in sensory-attentional processing but is correlated with either outcome contingencies, gain functions, decision outputs or motor planning, all processes that our decision-theoretic approach indicates are critical in choice behaviour.

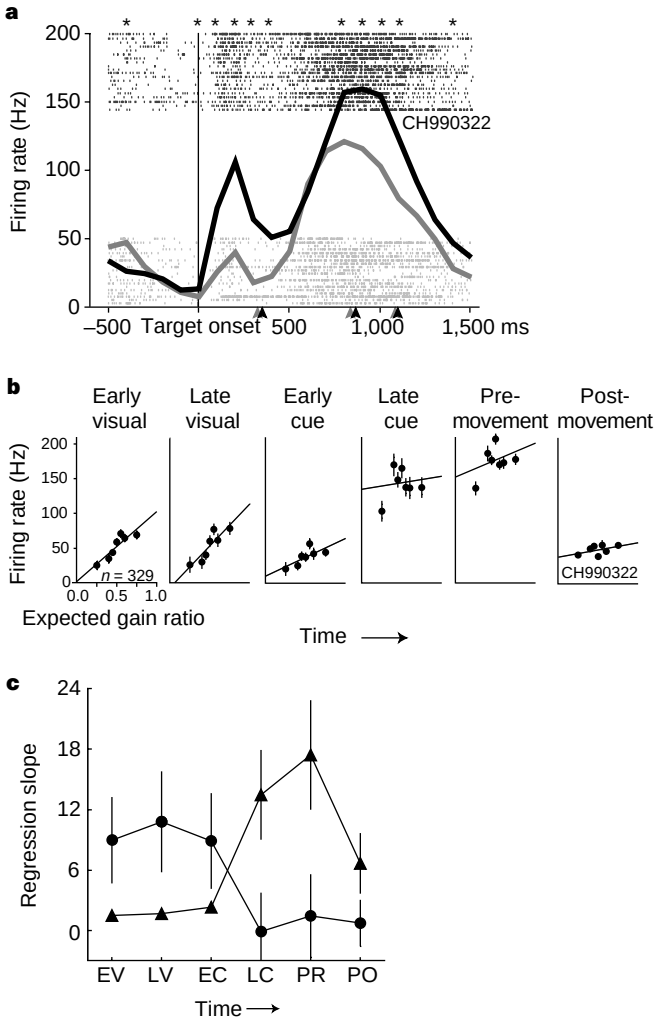

Figure 1 Modulation of neuronal activity by expected gain. The volume of juice delivered for each response was varied across blocks of cued saccade trials. **a**, Firing rate of an intraparietal neuron on trials instructing gaze shifts into the response field, averaged in 100 ms bins and synchronized, at vertical line, on target onset. Thick black line, expected gain ratio = 0.75 (n = 48); thick grey line, expected gain ratio = 0.25 (n = 37). Raster panels show spike times during the first 20 high-gain (dark grey) and first 20 low gain (light grey) trials. Panels show individual trials in sequential order from top to bottom. Arrows plot, successively, mean times of instruction cue onset, central fixation stimulus offset and saccade onset during high- (black arrow) and low- (grey arrow) gain blocks. Stars indicate 100-ms bins in which firing rate was significantly different in the high-gain block than in the low-gain block (t-test, $P < 0.05$). **b**, Mean firing rate (± s.e.) during each interval plotted against expected gain ratio, for all trials instructing gaze shifts into the neuronal response field. Lines indicate best-fit linear regressions through the raw data. **c**, Mean (± s.e.) regression slope for expected gain (circles) and the instructed movement (triangles), plotted against time (n = 40 neurons). Intervals: EV, early visual; LV, late visual; EC, early cue; LC, late cue; PR, pre-movement; PO, post-movement.

Experimental design

Here we examine whether a decision-theoretic model might reveal a link between the activity of area LIP neurons and the choices animals make in an oculomotor task. In the first experiment (experiment 1; Figs 1, 2), we monitored the activity of single intraparietal neurons while animals performed cued saccade trials, in which a change in the colour of a centrally located fixation stimulus instructed subjects to make one of two possible eye-movement responses in order to receive a juice reward. Before this stimulus changed colour, the rewarded movement was ambiguous. In successive blocks of trials, we varied either the volume of juice delivered for each instructed response (expected gain) or the probability that each possible response would be instructed (outcome probability), while holding all sensory signals and motor-related variables constant. This allowed us to test whether any portion of the variation in area LIP spike rates observed under these conditions was correlated with variations in the decision variables we manipulated.

In the second experiment (experiment 2; Figs 3, 4), animals were rewarded for choosing either of two possible eye-movement responses. In sequential blocks of trials, we varied the gain that could be expected from each possible response and then used the frequency with which the animal chose each response as an estimate of the subjective value of each option. This permitted us to test whether neural activity in area LIP was correlated with a behaviourally derived estimate of response value. Our data indicate that some of the variation in the LIP activity was, in fact, correlated with economic decision variables and that these variables influenced the choices made by our animal subjects and neural activity in a similar manner.

Decision variables and LIP spike rates

Figure 1a shows the activity of an intraparietal neuron on visually identical cued saccade trials during which the monkey was instructed to shift gaze into the neuronal response field for a juice reward. When, in one block of trials (thick black line), 0.26 ml of juice was delivered, this neuron was more active than when the same movement was made in response to the same visual display but during a block (thick grey line) in which only 0.09 ml of juice was delivered. This neuron was studied while expected gain was systematically varied across seven blocks of trials, and behavioural performance was maintained at 91% correct. To quantify the effects of these manipulations on the activity of this neuron, we computed average firing rates in six 200-ms epochs during each trial (early visual: 0–200 ms after the onset of the two response targets; late visual: 200–0 ms before the central light-emitting diode (LED) changed colour; early cue: 0–200 ms after the central LED identified the movement that would be reinforced; late cue: 200–0 ms before the command to initiate the movement; pre-movement: 0–200 ms before saccade onset; post-movement: 0–200 ms after saccade onset). Figure 1b shows the firing rate of this neuron (mean ± s.e.) as a function of the gain (in ml of juice) expected for a movement into the response field, divided by the sum of the

Table 1 Percentages of recorded neurons showing significant correlations between firing rate and expected gain, outcome probability or estimated value

Decision variable	Early visual/fixation*	Late visual/fixation*	Early cue/visual*	Late cue/visual*	Pre-movement	Post-movement	Total
Expected gain	27.5% (17.5%)	32.5% (15%)	40% (27.5%)	27.5% (62.5%)	30% (72.5%)	15% (65%)	62.5% (87.5%)
Outcome probability	35% (10%)	35% (10%)	40% (40%)	15% (100%)	30% (95%)	15% (95%)	75% (100%)
Estimated value	28% (6%)	17% (28%)	28% (47%)	19% (67%)	19% (67%)	25% (69%)	56% (89%)

Each entry indicates the percentage of cells in each experiment showing significant ($P < 0.05$) modulations in firing rate during each interval. Entries in parentheses indicate the percentage of cells that showed significant modulations in firing rate by the movement actually made by the animal. Total percentages indicate the percentage of neurons showing a significant modulation in firing rate during any interval. Asterisks identify the names of intervals measured in experiment 2 (early fixation, late fixation, early visual, late visual).

gain (in ml) available from both possible movements, for all those trials in which the animal shifted gaze to the target inside the response field of the neuron. The firing rate of this intraparietal neuron was correlated with this expected gain ratio early in the trials (early visual, $r = 0.432$, $P < 0.0001$; late visual, $r = 0.372$, $P < 0.0001$; early cue, $r = 0.217$, $P < 0.0001$), but later in the trials, around the time of the movement, firing rate and expected gain ratio were uncorrelated. These data indicate a temporal shift in the information encoded by this neuron, from expected gain early in trials to the movement made by the animal at the end of trials. On these same trials, movement amplitude ($r = -0.055$, $P > 0.322$), movement latency ($r = 0.016$, $P > 0.767$) and movement velocity ($r = 0.02$, $P > 0.718$) were uncorrelated with expected gain.

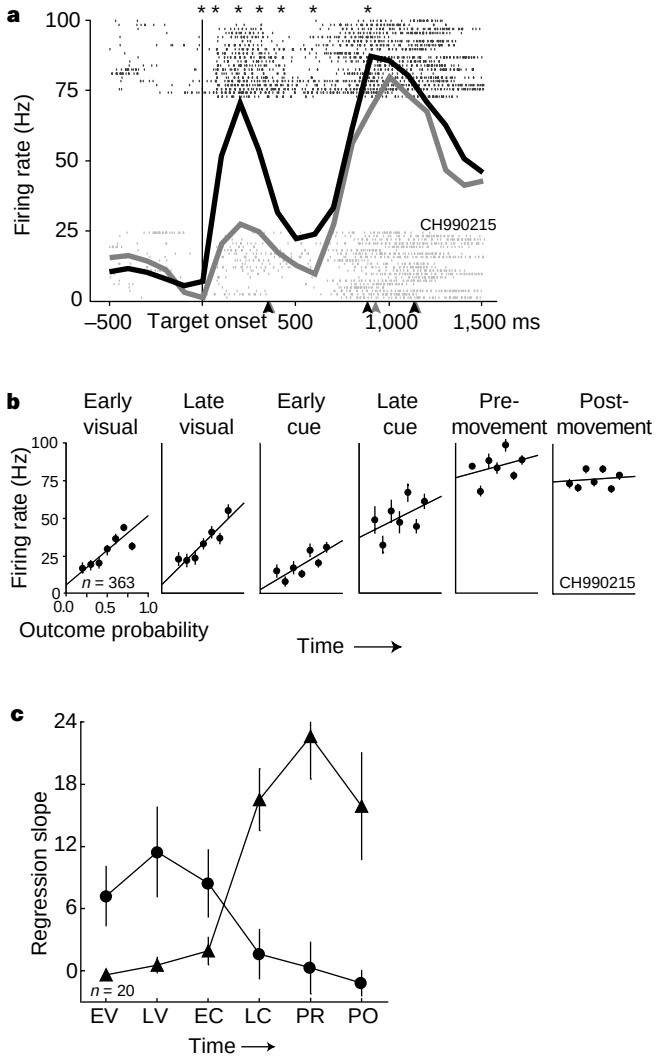

Figure 2 Modulation of neuronal activity by outcome probability. The probability that each response would be instructed was varied across blocks of cued saccade trials. **a**, Firing rate of an intraparietal neuron on trials instructing a gaze shift into the response field, as in Fig. 1. Thick black line, outcome probability = 0.80 ($n = 77$); thick grey line, outcome probability = 0.20 ($n = 26$). **b**, Mean firing rate (± s.e.) during each interval plotted against outcome probability, for all trials instructing gaze shifts into the neuronal response field. **c**, Mean (± s.e.) regression slope for outcome probability (circles) and the instructed movement (triangles) plotted against time ($n = 20$ neurons).

Each of 40 intraparietal neurons recorded from the brains of three monkeys was tested in 3–7 blocks of trials (mean = 4.7) in which the gain associated with each of the two target LEDs was different. For each neuron, correct trials were sorted into two groups based on whether the cued movement was into or out of the response field. For all trials in which the subject shifted gaze towards the response-field target, we analysed the relationship between firing rates computed during each interval described above and four variables: expected gain; the amplitude of each saccade; the average velocity of each saccade; and the latency of each saccade. We used a multiple regression analysis to determine which portion of firing-rate modulation could be uniquely attributed to changes in expected gain independently of changes in any of the three remaining movement-related variables. For comparison, a second multiple regression analysis was performed to determine the degree to which the firing rate of each neuron was uniquely influenced by which movement the subject was cued to make, after correcting for the effects of expected gain, movement amplitude, movement latency and movement velocity.

The slopes generated by the multiple regression analyses were used as an index of how strongly changes in expected gain modulated the activation of intraparietal neurons, independently of changes in movement amplitude, latency and velocity. Figure 1c shows the mean regression slope (± s.e.) for 40 intraparietal neurons for expected gain (circles); the mean slopes for the instructed movement (triangles) are provided for comparison. The regression slopes for expected gain were significantly greater than zero (single-sample t-test, $P < 0.05$) during the early visual and late visual intervals; expected gain strongly modulated the activation of the population of intraparietal neurons early in trials, before the identification of the rewarded movement. After the rewarded movement was identified, however, the activation of the intraparietal population was strongly modulated by the instructed movement, but not by expected gain.

Table 1 shows the percentages of neurons in this sample that were significantly modulated by expected gain during each interval, with the percentages of neurons significantly modulated by the instructed movement in each interval provided in parentheses for comparison. Overall, 62.5% of parietal neurons carried statistically significant information about expected gain at some point during the trial, and 87.5% of neurons carried statistically significant information about which movement was actually made. These data indicate that the activation of the intraparietal neuronal population is correlated with expected gain ratio, particularly during periods of uncertainty early in trials when decision variables might be important in formulating a movement plan.

Figure 2a shows the modulation of the activity of an intraparietal neuron by changes in outcome probability during visually identical cued saccade trials. When a saccade into the response field was instructed with a probability of 0.8 (thick black line), the neuron was more active than when an equivalent movement was instructed with a probability of 0.2 (thick grey line). This neuron was studied while outcome probability was varied across seven blocks of trials, and behavioural performance was maintained at 85% correct. Figure 2b shows the firing rate of this neuron (mean ± s.e.) as a function of outcome probability during each of the six measured epochs, for all trials on which the animal was instructed to shift gaze to the response field of the neuron. During the early visual ($r = 0.407$, $P < 0.0001$), late visual ($r = 0.349$, $P < 0.0001$), early cue ($r = 0.242$, $P < 0.0001$), late cue ($r = 0.131$, $P < 0.012$) and pre-movement intervals ($r = 0.116$, $P < 0.027$), firing rate increased with increases in outcome probability. Movement amplitude ($r = 0.056$, $P > 0.291$), latency ($r = -0.098$, $P > 0.061$) and velocity ($r = 0.07$, $P > 0.183$) were not correlated with outcome probability. The activity of this neuron was thus correlated with the probability that the animal would be instructed to choose each response, independent of the movement actually made by the animal.

We studied the effects of varying outcome probability across 5–7 blocks of trials (mean = 6.7) on 20 intraparietal neurons in two monkeys. Overall, 75% of the intraparietal neurons in our sample carried significant information about outcome probability at some point during the trial, while all 20 neurons carried significant information about which movement was actually made (Table 1). Figure 2c shows the mean (± s.e.) regression slopes for outcome probability (filled circles) and the instructed movement (filled triangles) for our population. The regression slopes for outcome probability were significantly greater than zero during the early visual, late visual and early cue intervals (single-sample *t*-tests, $P < 0.05$). The movement made by the animal significantly modulated neuronal activity in this population only after the cue identified the reinforced movement (late cue, pre-movement and post-movement intervals, single-sample *t*-tests, $P < 0.05$). The modulations induced by changes in outcome probability were very similar to those evoked by changes in expected gain and support the idea that outcome probability influences decision processes before the colour of the fixation stimulus identifies the reinforced movement.

Response value and LIP neural activity

The results of experiment 1 show that changes in either the gain expected from a particular response or the probability that a particular response will be required modulate the activity of intraparietal neurons. This is true even when all the visual and motor events associated with each trial are the same. In experiment 1, however, we were limited in our ability to assess the effects of expected gain and outcome probability on decision-making because there was a single correct choice identified in each trial, making it difficult to correlate any aspect of the choices made by our animal subjects with neuronal activity. In experiment 2, we therefore omitted the centrally located colour cue that identified only one of the responses as reinforced and instead allowed subjects to choose either of the two responses while we systematically varied the gain that could be expected from each response across 5–7 blocks of trials (mean, 5.8). The actual choices made by subjects were then used as an estimate of the valuation of each response by the animal on each trial and neuronal data was related directly to this behavioural readout of the animal's decision process.

Figure 3a shows, for visually identical trials in which the animal chose to shift gaze into the response field of the neuron under study, the modulation in activity of an intraparietal neuron in this free-choice task. The neuron was more active during a block of trials rewarded with 0.15 ml of juice (Fig. 3a, thick black line) than in another block of trials in which the same movement was rewarded with only 0.05 ml of juice (Fig. 3a, thick grey line). In fact, during the high-gain block the neuron became activated before the onset of the two choice targets, a pattern of activation that cannot be attributed to a visual response to target onset.

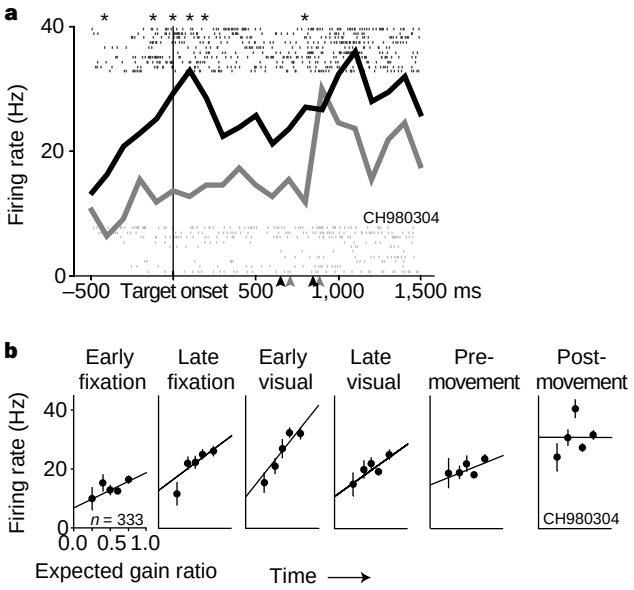

Figure 3 Modulation of the activity of a single intraparietal neuron by expected gain in a free-choice task. The volume of juice delivered for each response was varied across blocks of saccadic choice trials. **a**, Firing rate of an intraparietal neuron on trials in which subjects chose to shift gaze into the response field, as in Fig. 1. Thick black line, expected gain ratio = 0.75 ($n = 75$); thick grey line, expected gain ratio = 0.25 ($n = 11$). Raster panels plot spike times during the first 10 trials in both the high-gain (dark grey) and low-gain (light grey) blocks. Arrows plot, sequentially, the mean times of central fixation stimulus offset and saccade onset in high- (black arrows) and low- (grey arrows) gain blocks. **b**, Mean firing rate (± s.e.) during each interval plotted against expected gain, for movements into the response field.

We also measured the average firing rate of this neuron during six 200-ms epochs (early fixation, late fixation, early visual, late visual, pre-movement and post-movement). Figure 3b shows the firing rate of this neuron (mean ± s.e.) during these epochs (note that two of these intervals, early fixation and late fixation, are before the illumination of the visual targets). Firing rate increased with expected gain during the early fixation ($r = 0.158$, $P < 0.025$), late fixation ($r = 0.181$, $P < 0.01$), early visual ($r = 0.263$, $P < 0.001$) and late visual ($r = 0.187$, $P < 0.01$) intervals, but not around the time of the movement.

These data confirm the correlation between neuronal activation and the gain that could be expected from a particular movement, as reported in the previous experiments. The goal of this experiment, however, was to directly correlate neuronal activity with the animal's estimate of the value of the two possible movements. Figure 4a presents the choices the subject made across all blocks of trials during this recording session. Consistent with Herrnstein's matching law[14] for choice behaviour, there was a linear relationship between the proportion of trials on which the animal chose the target inside the response field and the proportion of total juice available for gaze shifts to that target ($r = 0.96$, $P < 0.008$)[35,36]. Across 36 data sets, there was a high correlation between the frequency with which monkeys shifted gaze to a target and the proportion of total juice available for gaze shifts to that target (mean $r = 0.89$, mean $P = 0.03$, mean slope = 1.86, mean intercept = −0.45). Thus, the choice behaviour of our subjects reliably reflected the gain

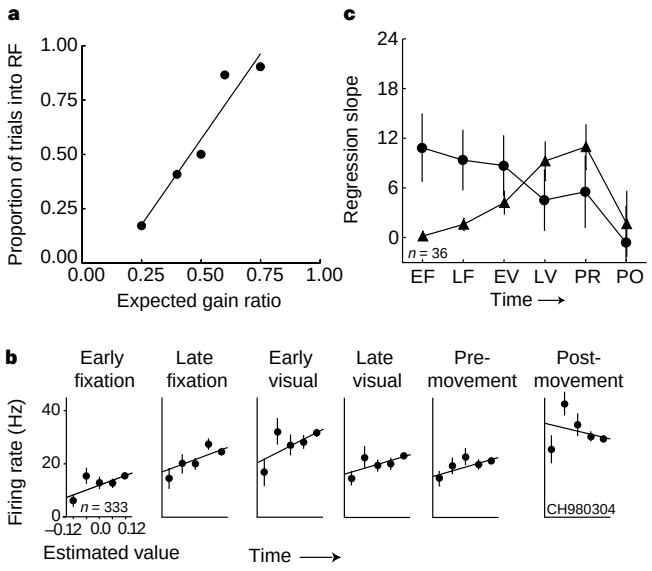

Figure 4 Correlation of firing rate with a behavioural estimate of the subjective value of the two movements. **a**, Proportion of trials on which the monkey chose the target inside the neuronal response field plotted against expected gain. Line indicates best-fit linear regression. **b**, Mean firing rate (± s.e.) during each interval plotted against a behavioural estimate of the subjective value of each response, computed on each trial from the difference in the reinforcement rates obtained from the two possible movements during the preceding 10 trials[24]. **c**, Mean (± s.e.) regression slope for estimated value (filled circles) and the chosen movement (filled triangles) plotted against time ($n = 36$ neurons). Intervals as in Fig. 1c, except: EF, early fixation; LF, late fixation.

associated with each movement. In subsequent analyses, we therefore used choice frequencies as an estimate of the subject's relative valuation of the two reinforced responses.

To analyse the relationship between the trial-by-trial activity of this neuron and the valuation of each choice by the subject, on each trial we computed a behavioural estimate of the subjective value of a movement into the response field, based on Herrnstein's melioration theory[23], by computing the difference in the rate of reinforcement the animal had obtained from each of the two possible choices over the preceding 10 trials (estimated value). Figure 4b shows the mean firing rate of the neuron as a function of this estimated value, during each measured interval, for all trials on which the animal shifted gaze into the response field. The firing rate of this neuron increased as the estimated value of a movement into the response field increased during the early fixation ($r = 0.204$, $P < 0.004$), late fixation ($r = 0.152$, $P < 0.031$), early visual ($r = 0.180$, $P < 0.01$) and pre-movement ($r = 0.144$, $P < 0.04$) intervals. The firing rate of this neuron was uncorrelated with saccade amplitude, velocity and latency during all six measured intervals, and thus these motor variables cannot account for the relationship between firing rate and the subjective value of a movement into the response field.

We recorded the activity of 36 intraparietal neurons from two monkeys performing this free-choice task. Overall, the regression slopes for estimated value were significantly greater than zero, at some point during trials, for 56% of the neurons in the parietal population, while the regression slopes for the chosen movement were significantly greater than zero for 89% of the population (Table 1). Figure 4c shows the mean (± s.e.) regression slope for the estimated value of a movement into the response field (circles) during each epoch, as well as the mean (± s.e.) regression slope for the chosen movement (triangles). The estimated value of a movement into the response field significantly modulated activity in our intraparietal neuronal population during the early fixation, late fixation and early visual epochs (single-sample t-tests, $P < 0.05$). The movement chosen by the animal significantly modulated activity in this same population of neurons during the late fixation, early visual, late visual and pre-movement epochs. Thus, when an animal is presented with a choice between two possible saccadic gaze shifts, the animal's estimate of the relative value of these two movements is correlated with the activation of intraparietal neurons. The activation of intraparietal cortex therefore appears to reflect the decision processes animals use to guide behaviour.

Discussion

Our results indicate that a decision-theoretic model of the sensory–motor process may provide a powerful alternative approach to traditional sensory and motor neurophysiological models of response selection. Experiment 1 indicates that both the gain expected from a particular response and the probability that a particular response will be required systematically increase the activation of neurons in posterior parietal cortex. Furthermore, this influence is separable from the effects of the immediate visual environment and from the neural events that govern movement dynamics. The effects of expected gain and outcome probability were strongest before the time at which the animal knew which of the two possible responses would be rewarded. Experiment 2 shows that when an animal is free to choose between alternative responses, the gain expected from each possible action exerts a correlated influence on both the choice behaviour of the animal and the activation of posterior parietal neurons. In our free-choice task, both monkeys and posterior parietal neurons behaved as if they had knowledge of the gains associated with different actions. These findings support the hypothesis that the variables that have been identified by economists, psychologists and ecologists as important in decision-making are represented in the nervous system.

Our data are, however, difficult to reconcile with traditional sensory-attentional or motor-physiological models. For example, sensory-attentional models typically attribute modulations in the activity of visually responsive neurons to changes in the behavioural relevance of visual stimuli[26] and, based on these models, it could be argued that our manipulations of expected gain and outcome probably merely altered the visual activity of intraparietal neurons. This interpretation seems unlikely for two reasons. First, when an animal is instructed to plan a gaze shift to one of two simultaneously presented eccentric visual stimuli, intraparietal neurons are insensitive to changes in the behavioural relevance of either stimulus when it is not the target of a saccade[34]. Second, in experiment 2 we showed that intraparietal neuronal activity was modulated by changes in the estimated value of each response during the fixation intervals before the onset of the response targets, when subjects were fixating the central LED in otherwise total darkness. We find this pattern of activation difficult to attribute to an attentional modulation of visually evoked activity.

It might also be suggested that the modulations in neuronal activity we evoked by changes in expected gain, outcome probability and estimated value reflect changes in the degree to which animals plan particular movements. Choice behaviour, such as that shown by subjects in experiment 2, might thus reflect the outcome of a covert competition between movement plans weighted by the estimated value of each possible action. However, because such a model must include an estimate of response value it is essentially equivalent to a decision-theoretic model.

Although the decision variables we have examined here systematically modulated the activity of intraparietal neurons in our tasks, these effects were, for most neurons, confined to the early portions of each trial. Late in each trial, intraparietal neurons were more strongly modulated by the animal's movement plan than by expected gain, outcome probability or the animal's estimate of response value. This may indicate that intraparietal cortex lies close to the motor output stages of the sensory–decision–motor process.

These data may also indicate that other brain areas believed to participate in decision-making, such as prefrontal cortex[37], might represent decision variables throughout the trial.

In conclusion, our results indicate that a neurobiological framework for the study of choice based upon the same classical decision theory that has guided behavioural studies of the choices humans and animals make may provide a powerful paradigm for studying the sensory–decision–motor process. Moreover, this framework indicates that many of the modulatory influences attributed to sensory attention or motor planning might be more precisely described as a reflection of decision processes. The influence of these variables on the activity of posterior parietal cortex, a brain area believed to participate in the transformation of sensory signals into motor commands, indicates that a decision-theoretic framework might be a useful tool for understanding the neurophysiology of sensory-guided behaviour. □

Methods

Single intraparietal neurons were studied in the brains of three rhesus monkeys trained to perform eye movements, in response to visual cues, for a fruit juice reward. Standard electrophysiological, behavioural and histological techniques were employed, as described[34]. All procedures were approved by the New York University Animal Care and Use Committee and were in compliance with the Public Health Service's *Guide for the Care and Use of Animals*.

Each experiment began with the electrophysiological isolation of a single intraparietal neuron. Animals were then instructed to make a series of 50–200 eye movements from a central starting position to successively illuminated LEDs randomly selected from among several hundred LEDs located at different peripheral positions. We used these movements to identify an eccentric LED that elicited a movement for which the neuron was maximally active (a movement into the response field) and an eccentric LED that elicited a movement for which the neuron was minimally active (a movement out of the response field).

Experiment 1. For experiment 1, this mapping procedure was followed by a series of cued saccade trials in total darkness. Each of these trials began with the illumination of a yellow LED located directly in front of the animal. A random interval (200–500 ms) after the subject had aligned his gaze (±2°) with this LED, the two eccentric yellow response LEDs identified by our mapping procedure were illuminated. After another random interval (200–800 ms), the central LED changed colour to either red or green, instructing the subject that a saccade aligning gaze with either the upper or lower eccentric LED, respectively, would be rewarded with a drop of juice. After a final random interval (200–800 ms), the central LED was extinguished and the monkey was rewarded if he shifted gaze into alignment with (±4°) the correct eccentric LED. We then determined whether the activation of intraparietal neurons was modulated by systematic changes in the gain expected from each possible movement or the probability that each of the two possible movements would be instructed. Animals typically performed this task correctly on about 90% of trials.

Expected gain. While each of 40 neurons was studied we varied, in 3–7 sequential blocks of about 100 trials each, the amount of juice reward the animals received both for movements into and movements out of the response field (expected gain). Across blocks, the sum of the juice available from these two possible movements was held constant, and the probability that either response would be instructed on a given trial (outcome probability) was held constant at 0.5. An experiment typically began with a block in which each movement was reinforced equally, and then pairs of blocks of complementary high gain/low gain conditions were randomly interleaved.

Outcome probability. While each of 20 neurons was studied we varied, in 5–7 sequential blocks of about 100 trials each, the probability that each of the two responses would be instructed while the gain expected from each movement was held constant. A block in which each movement was instructed equally often was typically run first, and then pairs of blocks with complementary high probability/low probability conditions were randomly interleaved.

Experiment 2. Thirty-six neurons were studied in two rhesus monkeys performing saccadic choice trials, which were similar to cued saccade trials but had no centrally located colour cue. Each of these trials began with the illumination of a yellow LED located directly in front of the animal. 500 ms after the subject had aligned his gaze (±2°) with this LED, the two eccentric yellow response LEDs identified by our mapping procedure were illuminated. After a random interval (500–800 ms), the central LED was extinguished and the monkey was rewarded if he shifted gaze into alignment with (±4°) either eccentric LED. The gain that could be expected from each movement was varied systematically across 5–7 blocks of about 100 trials each. A block in which each movement was reinforced equally was typically run first, and then pairs of blocks of complementary high gain/low gain conditions were randomly interleaved.

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