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RESEARCH NOTE

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# Behavioral reactions reflecting differential reward expectations in monkeys

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**Abstract** Learning theory emphasizes the importance of expectations in the control of instrumental action. This study investigated the variation of behavioral reactions toward different rewards as an expression of differential expectations of outcomes in primates. We employed several versions of two basic behavioral paradigms, the spatial delayed response task and the delayed reaction task. These tasks are commonly used in neurobiological studies of working memory, movement preparation, and event expectation involving the frontal cortex and basal ganglia. An initial visual instruction stimulus indicated to the animal which one of several food or liquid rewards would be delivered after each correct behavioral response, or whether or not a reward could be obtained. We measured the reaction times of the operantly conditioned arm movement necessary for obtaining the reward, and the durations of anticipatory licking prior to liquid reward delivery as a Pavlovian conditioned response. The results showed that both measures varied depending on the reward predicted by the initial instruction. Arm movements were performed with significantly shorter reaction times for foods or liquids that were more preferred by the animal than for less preferred ones. Still larger differences were observed between rewarded and unrewarded trials. An interesting effect was found in unrewarded trials, in which reaction times were significantly shorter when a highly preferred reward was delivered in the alternative rewarded trials of the same trial block as compared to a less preferred reward. Anticipatory licks preceding the reward were significantly longer when highly preferred rather than less preferred rewards, or no rewards, were predicted. These results demonstrate that behavioral reactions preceding rewards may vary depending on the predicted future reward and suggest that monkeys differentially expect particular outcomes in the presently investigated tasks.

**Keywords** Reaction time · Licking · Reward · Preference · Delayed response task · Monkey

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## Introduction

Learning theories postulate that conditioning consists of acquiring the expectation that a particular outcome will follow a particular event (Spence 1956; Bindra 1968), or that in the presence of a particular event, a particular response will result in a particular outcome (Tolman 1932). Early investigations used general observations of behavior to show that animals expect outcomes and that these expectancies can refer to specific magnitudes or kinds of rewards (Michels 1957; Hyde et al. 1968). Thus, when an expected outcome changes, the animal's behavior changes as well. For example, when rats are first exposed to a given magnitude of reward for a certain period of time and then a sudden shift in the reward magnitude occurs, the running time of rats in a runway changes dramatically (Crespi 1942). In a similar way, animals may expect particular kinds of reward. When food rewards following correct responses in a delayed response task are suddenly different from what they used to be, monkeys show clear signs of surprise and anger (Tinklepaugh 1928). Expectations of outcome can be advantageous also during learning if animals perform different reactions for different outcomes, as different expectations develop for different outcomes (Trapold 1970), even if one of the outcomes is nonreinforcement (Peterson and Trapold 1982). Thus differential outcome expectations may facilitate learning and discriminative performance by providing the subject with an additional source of information.

The goal of the present study was to examine the effects of predicted reward outcome on behavioral reactions in primates, using behavioral measures in tasks which test the executive functions of the prefrontal cortex and striatum. We studied two kinds of paradigms in which external cues predicted different outcomes. One kind of task involved an initial instruction cue which informed the animal about the spatial position of an upcoming movement target and the kind of food or liquid reward obtained for correctly performing the reaction. The other task involved a single movement target, and the instruction informed the animal whether a particular reward would be delivered or not for the correct reaction. The ability to expect a particular outcome early during the task would allow the animal to prepare different reactions depending on the outcome. The variability in outcome allowed us to examine to what extent expectations of different reinforcing events could be discriminably manifested in differential behavioral reactions leading to the outcome. We examined how different predicted rewards affected reaction times following presentation of the movement trigger and durations of anticipatory licking preceding reward delivery. We might expect that these measures reflect some of the motivational values of the expected rewards.

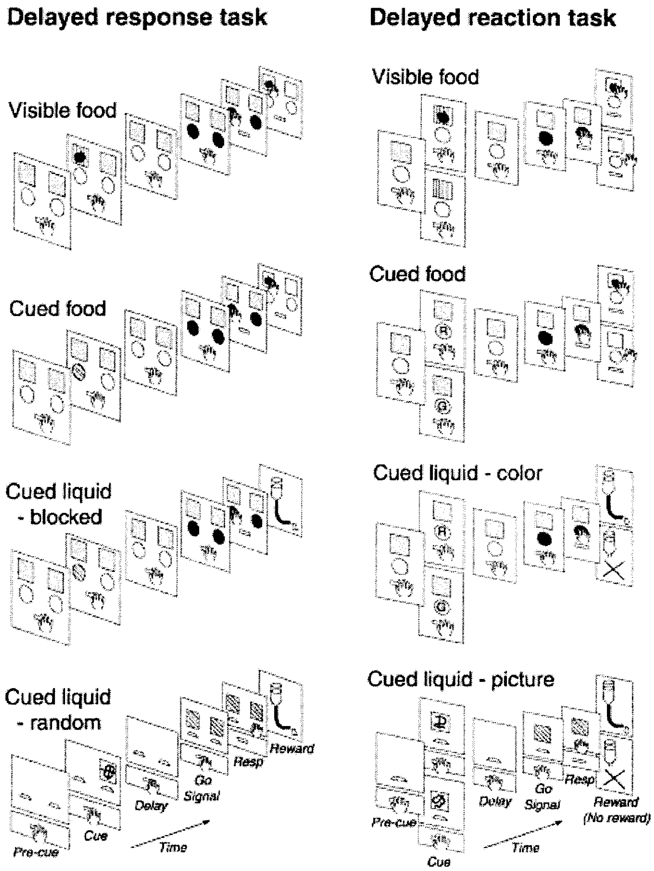


**Fig. 1** *Left:* Spatial delayed response task. Four versions were used (*top to bottom*): visible food, in which the food used in each trial block was shown at the onset of each trial; cued food, in which the food used in each trial block was indicated to the animal by using the same reward continuously within a block; cued liquid-blocked, in which the liquid used in each trial block was indicated to the animal by using the same reward continuously within a block; cued liquid-random, in which one of several liquids alternating semi-randomly in each trial block was indicated by a conditioned stimulus at trial onset. *Right:* Delayed reaction task with semi-randomly alternating rewarded and unrewarded trials. Four versions were used (*top to bottom*): visible food vs no food; cued food vs no food; cued liquid-color vs no liquid; cued liquid-picture vs no liquid. *R* indicates red light and *G* indicates green light

## Materials and methods

Five cynomologous monkeys (*Macaca fascicularis*), one female (A, weight 3.8 kg) and four males (B, C, D, E, weights 4.0–5.4 kg), and three male Japanese monkeys (*Macaca fuscata*; F, G, H, weights 5.5–6.5 kg) were used in the present experiments. They were cared for in the manner prescribed in the *Principles of laboratory animal care* (NIH publication No. 86–23, revised 1985) of the American Physiological Society. All the experiments were approved by the animal ethics committees in our institutions.

### Behavioral procedures

In order to study behavioral reactions in a range of comparable tasks, data were collected from different versions of spatial delayed response tasks and delayed reaction tasks. In each task, reproducible behavioral data were collected during neurophysiological recording experiments from two or three animals. The animals were seated in a primate chair with their head fixed and were returned to their home cages after each experimental day. In the different task versions, the animal faced a computer touch screen or a behavioral response panel with levers, liquid spouts, and food boxes. Each trial started when an instruction appeared for a brief period and indicated the spatial position of a future movement target and the reward received for correctly performing the movement, or no reward. After a short delay, a movement trigger stimulus was presented, and the animal touched the previously indicated target and received the predicted reward.

Trial outcome was varied by employing different food or liquid rewards, although some trial types went completely unrewarded. Pieces of about 0.5 g of raisin, sweet potato, cabbage, or apple served as food rewards and were presented in a food box in front of the animal, approximately at eye level. Drops of about 0.1–0.4 ml of water, refreshing isotonic beverage, and lemon, apple, orange, grenadine, or grape juice served as liquid rewards and were presented at a spout in front of the animal's mouth. In tasks using liquid rewards, animals received their daily liquid requirements while performing the tasks. Missing quantities of required liquids were given as water immediately after behavioral testing on each day. Water was available ad libitum during each weekend. Monkey pellets were available ad libitum at the home cage throughout the experiment, and more preferable foods were used as rewards in the laboratory.

### *Spatial delayed response task*

The reward used in each trial was either shown directly or cued by a visual instruction at trial onset. We used the following four task versions: *visible food*, *cued food*, *cued liquid-blocked*, and *cued liquid-random* (Fig. 1, left). The animal faced a panel which contained rectangular windows to the left and right of the midline, circular keys, and a holding lever below them. For the visible food task version, each window contained two screens: an opaque one and a transparent one with thin vertical lines. The animal first depressed the lever for 10–12 s, and the future food reward was presented to the left or right window behind the transparent screen. In the cued food and cued liquid-blocked task versions, a red light was presented for 1 s to the left or right key to indicate the side to be responded. After a delay of 5 s, a “go” signal of white lights appeared on both keys, and the animal was required to touch the key on the cued side within 2 s after the go signal. The same kind of reward was used in blocks of about 50 trials, and the animal could know what reward was used in a current block of trials after experiencing the currently used reward for 2 or 3 trials. Thus, different from the visible food task, the instruction cue of red light informed the animal of the future reward. These three kinds of tasks were used with animals F–H. In the cued liquid-random task version used with animals A, B, E, an instruction picture was shown on a computer screen to the left or right of the midline instead of the food windows and red lights, and it signalled different juices. Each instruction picture indicated a specific reward, and different rewards alternated semi-randomly between trials. Following a variable delay of 2.5–3.5 s, two identical red squares appeared as trigger stimuli on the screen. There were right and left keys located directly below the trigger stimuli, and the animal touched the key on the side previously indicated by the initial instruction. Trials lasted 12–14 s, with intertrial intervals of 4–6 s.

### Delayed reaction task

We used the following four task versions: *visible food*, *cued food*, *cued liquid-color*, and *cued liquid-picture* (Fig. 1, right). The animal faced a panel with a rectangular window, a circular key, and a holding lever arranged vertically. To start a trial, the animal depressed the lever for 10–12 s. In the visible food task version, the future food reward (rewarded trial) or the empty tray (unrewarded trial) was presented as instruction for 1 s in the window. After a delay of 5 s, a go signal of white light appeared on the key. The animal had to press the key within 2 s after the go singal. Correct lever press resulted in presentation of the food (rewarded trial) or the empty tray (unrewarded trial). The animal had to perform an unrewarded trial correctly to advance to a rewarded trial. Rewarded and unrewarded trials alternated semirandomly at a ratio of approximately 3:2. In the cued food and cued liquid-color task versions, a red or green light on the key indicated the presence or absence of a future reward, respectively. These three task versions were used with animals F–H. For animals C–E, the cued liquid-picture task version employed instruction pictures in the center of a computer screen to signal the presence or absence of a future reward, and the movement was elicited by a uniform red trigger square. Several different food and liquid rewards were employed in all task versions, but only a single kind of reward was employed in blocks of about 50 trials. This design permitted us to compare behavioral reactions in unrewarded trials between blocks using different rewards (the “missing” reward trials).

### Preference tests

Reward preferences of each animal were assessed in separate blocks of choice trials before or after behavioral testing in each animal. For animals A, B, E, two different instructions of the spatial delayed response task indicating two different liquid rewards were shown simultaneously at randomly alternating left and right target positions, allowing the animal to touch the lever of its choice following the trigger stimulus. All rewards were used in combinations in which animals showed reliable and persistent preferences. Thus, each pair of instruction stimuli contained one picture associated with a preferred reward and one with a nonpreferred reward. For animals F–H, preferences for different foods were assessed in free-choice tests by presenting several items at once to the animal. Preferences for different liquids were assessed by testing the animal's willingness to perform the task with one kind of reward after refusing to perform the task with another kind of reward.

### Data collection and evaluation

Data were collected after the initial 100–300 trials on each daily session. Many animals responded rather fast and irrespective of which reward was used at the start of many daily experiments. Therefore, always the same water reward was delivered, and only neurophysiological data unrelated to the present experiments were collected. Task performance became more differentiated after the initial 100–300 trials on each day, and clear differences related to motivational variables were observed. Data collection was stopped toward the end of each daily experiment when task performance became variable and motivation was reduced. Animals performed the tasks correctly in more than 95–98% of trials during data collection periods.

We assessed reaction times and durations of anticipatory licks as two independent behavioral indexes of expectation. We defined reaction time in animals A–E as the interval between onset of the movement-triggering stimulus and onset of the reaching movement (release of the holding lever by the animal's hand). In animals F–H, reaction time was defined as the interval between the movement-triggering stimulus and onset of target key pressing. We measured anticipatory licks in each trial with animals A–E by collecting interruption of an infrared light beam below the liquid spout by the animal's tongue at a rate of 2 kHz, and obtained sums of durations of interruptions during 2.0 s preceding onset of liquid reward delivery. Reaction time and lick data were pooled from several trial blocks from several sessions for 500–1,000 trials, separately for reward conditions and animals. Because of occasionally skewed distributions, we compared reaction times and durations of anticipatory licks between different outcomes by the nonparametric Kruskal-Wallis's $H$-test for multiple comparisons and the Mann-Whitney $U$-test for two-sample comparisons.

## Results

### Spatial delayed response task

Animals moved either to the left or right target depending upon the location of the instruction. Differences in reaction time between left and right targets were insignificant when the same food or liquid reward was used. However, reaction times differed significantly when different rewards were employed, being shorter for more preferred rewards among a given set of two or three rewards. Figure 2 (top) shows an example of reaction

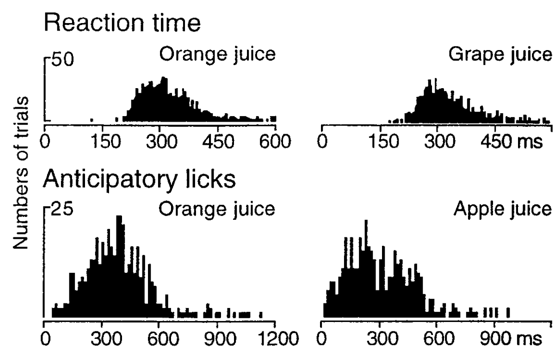


**Fig. 2** Examples of behavioral measurs differing between liquid rewards (cued liquid-random spatial delayed response task). *Top:* Histograms of reaction times for two different liquid rewards of different preferences in animal E (orange juice preferred over grape juice). Medians were, orange juice 304 ms (820 trials), grape juice 320 ms (737 trials). *Bottom:* Histograms of durations of anticipatory licking during 2.0 s preceding reward onset for two different liquid rewards in animal A (orange juice preferred over apple juice). Medians were, orange juice 371 ms (439 trials), apple juice 269 ms (424 trials); $P<0.001$ (Mann-Whitney test)

**Table 1** Reaction times in the spatial delayed response task (in milliseconds). Rewards 1(less preferred) and 2 (more preferred) were, respectively, for: animal A, apple and orange juice; animal B, grenadine and orange juice; animal E, grape and orange juice. In the cued liquid task version, rewards 1(less preferred), 2 (more preferred), and 3 (most preferred) were water, orange and grape juice for animal F, respectively, and water, refreshing isotonic beverage and grape juice for animals G–H, respectively. In the visible and cued food task versions, rewards 1, 2, and 3 were raisin, cabbage, and apple for animal F, respectively, whereas they were raisin, sweet potato, and cabbage for animals G–H, respectively. Values are medians (50th percentile) ± quartile deviations (75th to 25th percentiles/2) and are from movements to the left target

| | Reward 1 | Reward 2 | Reward 3 |
|---|---|---|---|
| Animal A | | | |
| Cued liquid-random | 365±49.0 | 319±30.0*** | |
| Animal B | | | |
| Cued liquid-random | 320±47.0 | 298±39.0*** | |
| Animal E | | | |
| Cued liquid-random | 320±41.0 | 304±36.0*** | |
| Animal F | | | |
| Cued liquid-blocked | 480±46.3*** | 450±30.0*** | 440±20.0*$^{++}$ |
| Visible food | 470±55.0*** | 410±25.0*** | 420±25.0*$^{+++}$ |
| Cued food | 530±52.5*** | 410±20.0*** | 420±20.0$^{+++}$ |
| Animal G | | | |
| Cued liquid-blocked | 420±16.3 | 410±20.0** | 420±20.0$^{+++}$ |
| Visible food | 410±23.8*** | 390±25.0*** | 400±25.0$^{+++}$ |
| Cued food | 420±25.0*** | 400±15.0*** | 410±25.5$^{+++}$ |
| Animal H | | | |
| Cued liquid-blocked | 620±65.0*** | 560±45.0*** | 560±40.0+++ |
| Visible food | 595±65.0*** | 560±55.0*** | 540±47.5**$^{+++}$ |
| Cued food | 580±65.0*** | 560±60.0 | 535±50.0**$^{+++}$ |

Mann-Whitney test: *$P$<0.05; **$P$<0.01; ***$P$<0.001 vs reward (indicated at left value, wrap around for reward 1 vs 3). Kruskal-Wallis test: $^{+}P$<0.05; $^{++}P$<0.01; $^{+++}P$<0.001 among 3 horizontally neighboring rewards

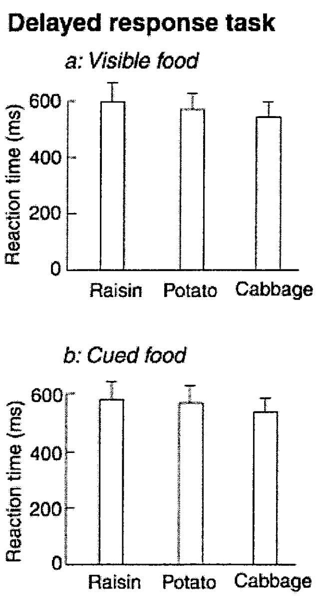


**Fig. 3a, b** Reaction times in different reward blocks in animal H during performance in the visible food (**a**) and cued food versions (**b**) of the spatial delayed response task. *Error bars* indicate quartile deviations

times of animal E observed when two different liquids (orange vs grape juice) were used in the cued liquid-random task version. Figure 3 shows reaction times of animal H during performance in the visible food and the cued food task versions. The differences in reaction time were seen in both task versions, and irrespective of whether foods or liquids were used as rewards. Table 1 shows median reaction time and quartile deviations for different rewards in each task for each animal. Median durations of anticipatory licks during 2.0 s preceding reward onset were significantly longer for more preferred liquid rewards, as compared to less preferred rewards, in animal A (Fig. 2, bottom) and in animal B (orange juice, preferred, median 749 ms, 985 trials, vs grenadine juice, 675 ms, 911 trials; $P$<0.005, Mann-Whitney test).

## Delayed reaction task

Animals moved to a single target located in the horizontal center ahead of them. Large and consistent significant differences in reaction time and anticipatory licking were seen between rewarded and unrewarded trials in every animal. Reaction times were shorter in rewarded than unrewarded trials, whatever reward was used in each trial block. Figure 4 (top) shows an example of reaction times of animal D in the cued liquid-picture task version. Figure 5 illustrates reaction times in the visible food and cued food task versions for animal G. The differences in reaction time were consistently seen in all task versions, and irrespective of whether foods or liquids were used as

**Table 2** Reaction times in the delayed reaction task (in milliseconds). The same reward was employed in blocks of about 50 trials to permit comparisons of movements in unrewarded trials depending on which reward was delivered in rewarded trials (the "missing" reward). Values are medians (50th percentile) ± quartile deviations (75th–25th percentiles/2). Reward 1 for monkeys C–E was apple juice. Rewards 1–3 for monkeys F–G were as in Table 1

| | Reward 1<br>No reward | Reward 2<br>No reward | Reward 3<br>No reward | Kruskal-Wallis test |
|---|---|---|---|---|
| Animal C | | | | |
| Cued liquid-picture | 318±30.0[a] | | | |
| | 454±90.0[b] | | | |
| Animal D | | | | |
| Cued liquid-picture | 354±36.0[a] | | | |
| | 458±74.0[b] | | | |
| Animal E | | | | |
| Cued liquid-picture | 276±31.0[a] | | | |
| | 427±57.0[b] | | | |
| Animal F | | | | |
| Cued liquid-color | 570±57.5[a]*** | 480±40.0[a]*** | 460±45.0[a] | +++ |
| | 885±196.3[b] | 800±135.0[b] | 800±195.0[b] | |
| Visible food | 480±58.8[a]*** | 440±30.0[a]*** | 435±30.0[a] | +++ |
| | 600±102.5[b]*** | 590±113.8[b] | 470±40.0[b]*** | +++ |
| Cued food | 460±47.5[a]*** | 440±20.0[a]*** | 430±20.0[a] | +++ |
| | 730±100.0[b]*** | 635±141.3[b]*** | 550±60.0[b]*** | +++ |
| Animal G | | | | |
| Cued liquid-color | 400±20.0[a]*** | 390±20.0[a]*** | 390±15.0[a] | +++ |
| | 670±115.0[b]*** | 610±95.0[b]* | 585±95.0[b]* | +++ |
| Visible food | 370±25.0[a]*** | 350±15.0[a]*** | 340±15.0[a]*** | +++ |
| | 535±80.0[b]*** | 500±80.0[b] | 440±53.8[b]*** | +++ |
| Cued food | 360±20.0[a]*** | 350±25.0[a]*** | 355±25.0[a] | +++ |
| | 450±70.0[b]** | 440±80.0[b] | 410±45.5[b]*** | +++ |
| Animal H | | | | |
| Cued liquid-color | 540±63.8[a]*** | 520±25.5[a]*** | 510±20.0[a] | +++ |
| | 800±76.3[b]*** | 730±105.0[b]*** | 720±91.3[b] | +++ |
| Visible food | 500±45.0[a]*** | 490±33.8[a]*** | 480±25.0[a]*** | +++ |
| | 600±75.0[b] | 595±65.0[b] | 590±50.0[b] | |
| Cued food | 510±30.0[a]*** | 510±30.0[a] | 500±33.8[a]* | + |
| | 570±60.0[b] | 580±43.8[b] | 560±45.0[b]*** | ++ |

[a] Rewarded trials
[b] Unrewarded trials
Reaction times were statistically significant ($P<0.001$; Mann-Whitney test) between rewarded and unrewarded trials for every reward in every animal. Pairwise comparisons between rewarded trials, or between unrewarded trials, are indicated at the leftmost rewarded or unrewarded trial block (wrap around for reward 1 vs 3: *$P<0.05$; **$P<0.01$; ***$P<0.001$; Mann-Whitney test). Comparisons among 3 horizontally neighboring rewards (or no reward conditions) are indicated by: $^{+}P<0.05$; $^{++}P<0.01$; $^{+++}P<0.001$ (Kruskal-Wallis test)

rewards. Median durations of anticipatory licks were considerably longer in liquid-rewarded as compared to unrewarded trials (Fig. 4, bottom).

In rewarded trials reaction times varied significantly between trial blocks with different rewards, comparable

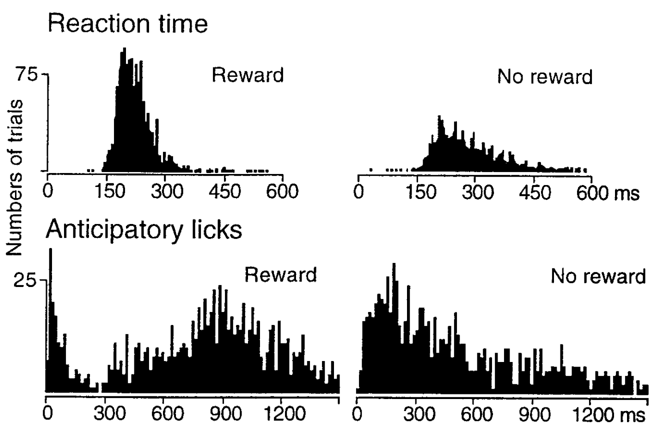


**Fig. 4** Examples of behavioral measures differing between rewarded and unrewarded trials (cued liquid-picture delayed reaction task). *Top:* Histograms of reaction times for liquid reward (apple juice) vs no reward in animal D. Medians were, reward 354 ms (1,374 trials), no reward 458 ms (992 trials). *Bottom:* Histograms of durations of anticipatory licking during 2.0 s preceding reward onset for liquid reward (apple juice) vs no reward in animal E. Medians were, reward 845 ms (1,028 trials), no reward 411 ms (924 trials); $P<0.001$ (Mann-Whitney test)

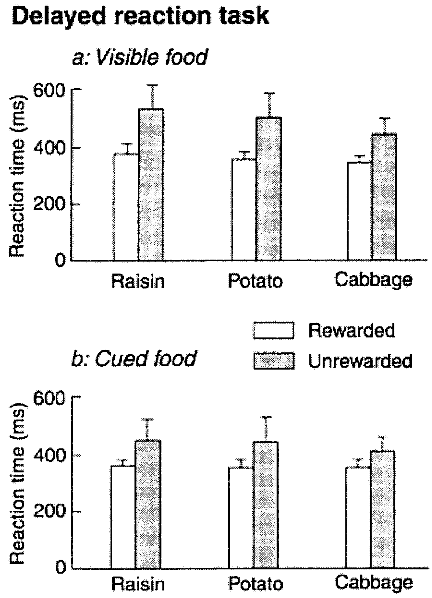


**Fig. 5a, b.** Reaction times in different reward blocks in animal G during performance in the visible food (**a**) and cued food versions (**b**) of the delayed reaction task. *Error bars* indicate quartile deviations

with the differences in the spatial delayed response task. Interestingly, in unrewarded trials reaction times varied also between trial blocks. The differences depended on which reward was used in each block. They were shorter in unrewarded trials when more preferred rewards were employed in the alternate trials within each block. This occurred despite the fact that the animal could not expect to obtain any reward in unrewarded trials, and that performance in unrewarded trials went unrewarded in exactly the same manner (presentation of vacant food tray or no delivery of liquid). Table 2 shows median reaction times and quartile deviations in rewarded and unrewarded trials for different kinds of rewards.

## Discussion

These data show that expectations of outcomes may influence behavioral reactions in several versions of tasks testing the executive functions of the primate frontal cortex and basal ganglia. Both reaction times and anticipatory licking varied between different expected rewards and, even more so, between rewarded and unrewarded trials. The behavioral reactions were more vigorous for rewards that were more preferred by the animals, suggesting a relationship to the motivational value of the rewards. Interestingly, behavioral reactions in unrewarded trials depended on the type of reward given in alternate trials of the same trial block. These data suggest that the animals discriminated between the different rewards and expected the type of reward produced by the movement.

### Behavioral task

As judged from the effects of lesions and neurophysiological recordings, the spatial delayed response paradigm tests the mnemonic and movement preparatory functions of the primate prefrontal cortex and the closely associated striatum (Jacobsen and Nissen 1937; Divac et al. 1967; Fuster and Alexander 1971; Kubota et al. 1974; Alexander 1987; Hikosaka et al. 1989a; Funahashi et al. 1993). The initial instruction cue determined the operant response to the subsequent movement trigger stimulus in the spatial delayed response task. It contained additional information about the predicted reward. In the delayed reaction task, the only differential information contained in the instruction concerned the predicted reward. In both tasks, the reward information was only incidental for correct task performance, as the animal was not required to perform an operant action based on the reward predicted by the instruction in order to obtain the reward. Thus the reward predictions of the instruction cues were classically (Pavlovian) conditioned. This description is valid for both the arm movement response and the licking measured presently. There were no limits in reaction time that would differentiate between the two rewards employed in individual trial blocks. Likewise, the animal was not required to lick in anticipation of the reward in order to receive it. Nevertheless, these incidental informations did control the behavioral reactions of the animal.

### Expectations and motivational value

Reaction times were consistently longer in unrewarded trials compared with rewarded trials in the delayed reaction task and longer for one particular reward compared with the other reward in both the spatial delayed response task and the delayed reaction task. This was true irrespective of whether the expected reward was the same liquid during a block of about 50 trials (cued liquid-blocked) or changed from trial to trial (cued liquid-random). Similar differences between rewarded and unrewarded movements were seen in a sequential movement task in which only the final movement was rewarded (Bowman et al. 1996).

Reaction times were shorter and anticipatory licks were longer for rewards that were more preferred by the animals, as assessed in choice trials or in reward-no reward comparisons. Thus preferred objects appeared to elicit faster and more intense behavioral reactions. However, it might be conjectured that the differences in behavioral reactions are due to different conditional requirements. This may hold for differences between the tasks but appears to be an unlikely explanation for behavioral differences within single tasks, as the only variations within each task was the kind or amount of reward delivered. It thus appears that the most likely explanation for the behavioral differences is related to the differential effect of reward expectation on behavior and probably reflects the differences in motivational value of the tested rewards.

Larger effects of expected outcome on reaction times were observed in trial blocks comparing rewarded with unrewarded trials, whereas comparisons between different food or liquid rewards showed usually less important differences. These variations in behavioral effects should reflect the larger differences in motivational value between the presence and absence of reward, as compared to the differences between individual rewards. The observed behavioral effects appear to be graded according to differences in motivational value, and comparisons between rewards producing less important differences in preference have smaller effects on behavioral reactions. Differences in behavioral reactions appear to be less important when different liquid rewards are compared in overtrained animals (Hassani et al. 2001).

Reaction times in the delayed reaction task differed among different trial blocks in the unrewarded trials depending on which reward was available in the rewarded trials of the same trial block. The differences between unrewarded trials were in general similar to those between rewarded trials (Table 2), although some larger variations were noted occasionally (Fig. 5). They occurred despite the fact that the outcome in unrewarded trials was always the same (no reward). Apparently a given trial block with its semi-randomly alternating rewarded and unrewarded trials constituted a context in which the reactions in one trial type were influenced by events in the other trial type. The shorter reaction times in unrewarded trials alternating with trials using more preferred rewards may indicate a generally increased level of motivation in these trial blocks, as compared to blocks in which less preferred rewards were used. It may be speculated that animals tried to finish the unrewarded situation more rapidly in order to advance to the more preferred reward.

## Mechanisms of outcome expectations

The influences of expected outcome on reaction time and lick duration suggest that animals have access to and use representations of individual expected outcomes. The representations were acquired through classically conditioned instruction-reward associations during previous experience, are specific for each reward, may be modulated by the context of a given trial block, and are evoked in each trial by the instruction cue. The influence of differential outcome representations would explain why the same behavioral response was executed slightly differently depending on the expected outcome. The differential representation of the outcome, as suggested by the present experiments, may lead to faster learning of differentially rewarded behavioral reactions and thus might help to explain the so-called “differential outcome effect” in which discriminative responses are learned faster when each response leads to a different reinforcer (Trapold 1970). The function of outcome representations during the execution of behavior directed at that outcome would fulfill one of the necessary conditions for the behavior to be goal-directed (Dickinson and Balleine 1994). According to this notion, the animal would perform the arm movement with the (implicit or explicit) knowledge that the specific reward indicated by the instruction would be obtained.

Reward expectations should exert their influence on behavior in structures involved in the preparation and execution of goal-directed behavior. Some neurons in the primate prefrontal cortex and striatum show correlates for the expectation of environmental events and are activated for several seconds during the expectation of reward (Hikosaka et al. 1989b; Watanabe 1990; Apicella et al. 1992; Schultz et al. 1992; Watanabe 1996; Tremblay and Schultz 1999). These structures contain also neurons whose activity is related to the preparation or execution of arm or eye movements. In particular, many of these behavior-related activities are influenced by the expected type of reward (Watanabe 1996; Hollerman et al. 1998; Kawagoe et al. 1998; Leon and Shadlen 1999; Hassani et al. 2001). Thus expected rewards may influence neuronal activities related to the behavior leading to the rewards (Schultz 2000), which suggests a neuronal mechanism contributing to the observed influences of expected rewards on the intensity of behavioral reactions.

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