Exp Brain Res (2003) 149:267–275
DOI 10.1007/s00221-002-1353-9

RESEARCH ARTICLE

Céline Amiez · Emmanuel Procyk · Jacques Honoré · Henrique Sequeira · Jean-Paul Joseph

Reward anticipation, cognition, and electrodermal activity in the conditioned monkey

Received: 5 June 2002 / Accepted: 15 November 2002 / Published online: 14 February 2003
© Springer-Verlag 2003

Abstract In the present report, we examine electrodermal activity (skin conductance responses, SCRs) in monkeys trained to perform target-selection (TS) tests. In each test, the animal was presented in successive trials with the same two unequally rewarded targets on a touch screen. The probabilistic contingencies of the rewards associated with each target rendered the selection of the best difficult. Our findings revealed SCRs time-locked to the arm movements toward the rewarded targets, occurring after the target touches. Parameters of the SCRs were stable when the uncertainty of the choices and of the outcomes varied. The results support the hypothesis that the physiological processes indexed by the SCRs are the correlate of anticipatory appetitive behavior. In contrast, there is no evidence that the SCRs reflect cognitive processes associated with the detection of the best target.

Keywords Target selection · Skin conductance responses · Electrodermal activity · Reward anticipation · Rhesus monkey

Introduction

The capacity to anticipate and to internally simulate the positive or negative consequences of action is a decisive aspect of behavior. This capacity allows us to interact more effectively with the environment and, if necessary, to modify our course of action. It is a fundamental condition of adaptive behaviors in complex or ambiguous environments.

C. Amiez (✉) · E. Procyk · J.-P. Joseph
Institut Fédératif des Neurosciences de Lyon,
Inserm U371, 18 ave Doyen Lepine, 69675 Bron, France
e-mail: amiez@lyon151.inserm.fr
Tel.: +33-4-72913494
Fax: +33-4-729134 61

J. Honoré · H. Sequeira
Laboratoire de Neurosciences du Comportement,
Université de Lille I, SN4.1, 59655 Villeneuve d'Ascq Cedex, France

Expectation and motor preparation can be launched by external or internal signals and are thought to require autonomic adjustments (Routtenberg 1968; Pribram and McGuinness 1975). Electrodermal activity (skin conductance responses, SCRs) is considered to reflect such adaptive mechanisms, anticipating the occurrence of a significant event (Boucsein 1992), i.e., an event of interest for the organism because of its uncertainty or its motivational value (reward or punishment).

The anticipation linked to an external signal has been investigated in many studies devoted to classical conditioning. In this paradigm, the unconditioned stimulus is initially followed by SCR changes. As the conditioning progresses and the neutral stimulus acquires a conditional value, such changes come to anticipate the imminent unconditioned stimulus. Considering that movement is known to influence SCRs (Culp and Edelberg 1966; Edelberg 1970; Siddle et al. 1979), the possibility that an action generating reward can be accompanied by specific SCR changes remains an open issue.

The aim of the present study was to investigate for the first time SCRs in a rewarded cognitive task in non-human primates. We show that SCRs precede food-reward delivery at the time of arm movements. We also investigate possible alterations of SCRs in cognition.

Materials and methods

Two male rhesus monkeys (monkeys E and N) were used in this experiment. They were originally prepared for extracellular electrophysiological unit recordings. In monkey E, the SCRs were investigated during a pause in the neuronal recordings. When the recording began, the animal had been trained in the tasks for 2 years. In monkey N, which had been trained for 4 months, the neuronal recordings had not yet begun. Monkey E worked with the left hand, while monkey N worked with the right hand. Monkey E worked head-fixed; monkey N worked head-free. In the two monkeys, surgical procedures were carried out according to the 1986 European Communities Council Directive (Ministère de l'Agriculture et de la Forêt, Commission Nationale de l'Expérimentation Animale).

The animal was seated in a primate chair in front of a tangent touch-screen (Microtouch System) coupled to a TV monitor. The

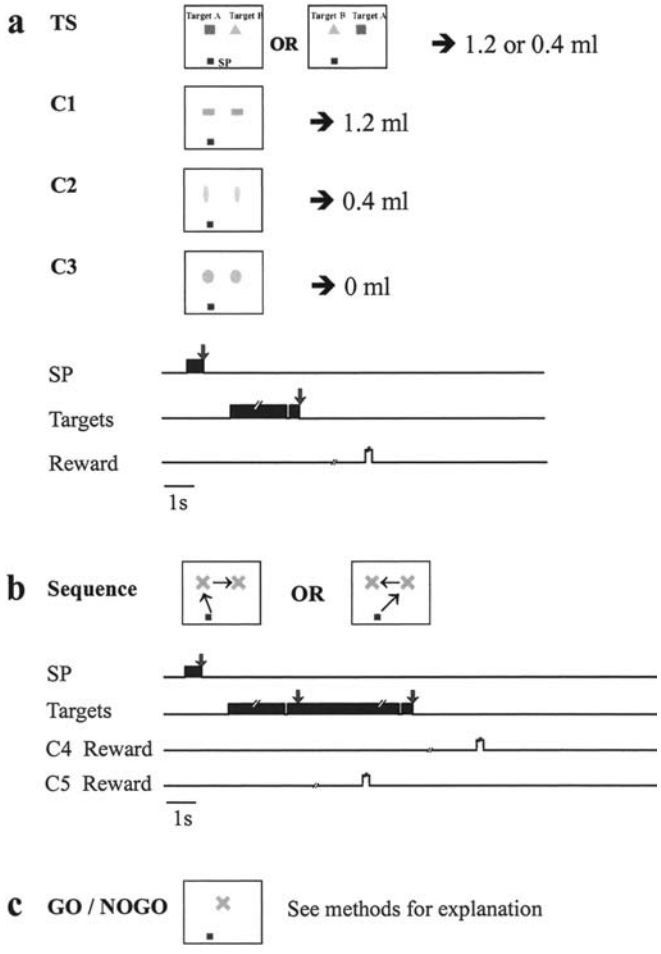


Fig. 1a, b Display and trial events in the target-selection (TS) task, in control tasks C1, C2, and C3 (**a**) and in the sequence task (**b**). Location of the two target positions on the display monitor. A 2×2 cm square located 10 cm below either one (randomly, 50/50) of the two targets served as starting position of the hand (*SP*; the left SP is represented). Gray areas correspond to the time of illumination of the lever and of the targets. *Arrows* indicate the responses of the animal. See Materials and methods section

screen was located at arm's length. In the front panel of the chair, an arm-projection window was opened, which allowed the monkey to touch the screen with one hand. Another smaller window was opened at the level of the nonperforming hand to record SCRs. A computer recorded the position and correctness of each touch. It also controlled the presentation on the monitor of visual stimuli (colored shapes), which served as light-targets (CORTEX software; NIMH Laboratory of Neuropsychology, Bethesda, Md.). Either one of two 2×2-cm white squares (located 10 cm below the targets on the left and on the right) was illuminated and served as starting position (SP) to initiate a trial. One SP was randomly chosen (50/50) by the computer in each trial (Fig. 1a).

Behavioral paradigm

When the monkey touched the SP, two targets A and B simultaneously appeared on two fixed, spatial virtual windows (6°x6°), centered on the horizontal plane at 10 cm to the right and to the left from the screen center. Each target was a combination of colored shapes and occupied either one (50/50) of the two windows randomly. After a 2- to 3-s delay period, the targets were briefly (100 ms) extinguished. This was the "GO" signal. The monkey was then allowed to release the SP and touch one target within the 1,000 ms following the GO signal. The target touch extinguished the two targets. The touch of either one of the targets was followed, 2–2.5 s later, by a squirt of fruit juice. The reward was followed by a 6-s time-out. One SP was then reilluminated for another trial. If the monkey released the SP before the GO signal, the trial was aborted. The monkey then had to resume the trial until successful completion.

Touching target A yielded 1.2 ml of juice, with probability P=0.7, and 0.4 ml, with probability P=0.3 (rewards of 1.2 ml and 0.4 ml corresponded, respectively, to a valve opening of 250 ms and 130 ms). The reinforcement ratio for target B was the opposite. These reward contingencies were implemented as follows. The animal performed successive blocks of 20 trials. In each block, all trials were randomly selected by the computer without repetition. In 14 trials, the choice of target A gave 1.2 ml and the choice of target B, 0.4 ml. In the other 6 trials, the rewards were the opposite. Systematic choice of target A corresponds to the best possible strategy. It gave, on the average, 0.7×1.2 ml+0.3×0.4 ml=0.96 ml per trial. This average reward value is the "value of the game." In this report, the best-rewarded target in a couple is named A. The systematic choice of target B gave, on the average, 0.3×1.2 ml+0.7×0.4 ml=0. 54 ml per trial and corresponds to the worst strategy. Any intermediate strategy combining choices of A and B gave intermediate average rewards proportional to the number of choices of A.

Within a test (or problem), we defined an "evaluation" period during which the animal searched for the best target by touching either one of the two targets and a "repetition" period during which he persistently chose the same target, generally the best. The beginning of the repetition period was defined as either (a) the beginning of the first period of 10 successive trials in which the animal touched the same stimulus (preferred target), or (b) the beginning of the first period of 11 successive trials in which the animal touched the preferred target 10 times and the other target once. In the latter case, an additional requirement was that the beginning of the period was made up of at least 5 successive touches of the preferred target. The probability, by chance alone, of touching the same target 10 times in a series of 10 successive choices is 1/1024, and the probability of touching the same target 10 times by chance alone, in case b, is less than 5/2048. Thus, the probability that a repetition period occurs by chance alone is less than 1% (7/2048=0.0034). We took this performance level to indicate that the animal had selected one particular target and that a decision regarding the best target had been reached. When the repetition period was terminated, two new targets were selected and another test was initialized. Free rewards of 1.2 ml or 0.4 ml were randomly given to the animal between the tests.

The two animals were also trained in three control tasks (C1, C2, C3) in which the quantity of reward was predictable. These tasks were similar to the TS task, but the difference was that the two targets were fixed and identical. In C1, touching the targets (two blue rectangles) was always rewarded with 1.2 ml; in C2 (two green ellipses), touching the targets was rewarded with 0.4 ml; in C3, touching the two red disks was never rewarded, but touching one was mandatory for the experiment to proceed to other tasks. The trials of task C3 were intermixed with trials of the TS tasks in the proportion of 1/10. Tasks C1 and C2 were given to the animal between the tests of the TS task.

Using a sequence of two movements in tasks C4 and C5 (monkey N), we further studied the relationships between dermal activity, sequence of movements, and reward schedule. When the animal touched the SP, he was presented with two fixed identical targets (green crosses) in the virtual windows used in the TS task (Fig. 1b). The animal had to touch the two targets in succession. There were two successive GO signals delivered by the two targets at the same time, one for the first touch and, 3.5–5.5 s later, one for the second. The monkey made first an arm movement from the lever toward the first target in response to the first GO signal. He then kept his hand on the first target and waited for the second GO signal to touch the second target. The targets could be touched only

after the GO signals. The animal had to find the correct order for touching the targets (left and then right, or right and then left) and repeat, in successive trials, the newly found order. There were two reward schedules: in C4, the first touch was rewarded with 0 ml and the second with 1.2 ml; in C5, the schedule was the opposite. The four combinations (order x reward schedule) randomly alternated every 5–6 correct trials. Each new combination was preceded by a warning signal (red flashing circle).

Monkey N was also trained in a GO-NOGO task to study the effect of selection errors on dermal activity. Following the touch of the SP, a single stimulus (a blue cross) was presented in the center of the screen (Fig. 1c) and was then briefly extinguished (GO signal) after 2–2.5 s. In the GO trials, the animal had to touch the target for liquid reward delivered 2–2.5 s after the touch. In the NOGO trials, he had to withhold the movement and keep touching the SP until reward delivery. The two types of trials randomly alternated every 5–8 correct trials. The end of one type of trials was announced by the lack of reward in the corresponding trials.

Electrodermal activity

The skin conductance responses (SCRs) were recorded from the non-performing hand, which was attached to a resting pad. The electrode attachment sites were cleaned with soap. Two Ag–AgCl Beckman dermal electrodes were positioned on the palmar surface and secured by means of double-stick collars. Electrodes were previously filled with a 0.05 M NaCl electrolyte, which follows recommendations by Fowles et al. (1981). The animal was grounded and the SCRs were recorded with a skin conductance coupler (Coulbourn Instruments, S71-23) using constant voltage. The skin conductance coupler was connected to a computer. The SCRs (measured in microsiemens, μS) were digitized at 250 Hz and stored.

Data analysis

In each trial of the TS tasks or of the control tasks, the identity A or B (location right or left) of the touched target, as well as the quantity of reward given to the monkey, were stored. Reaction times (RTs) and movement times (MTs) were computed.

To characterize the strategies used by the animal to find the best target, we considered, in a large population of tests, the choices made in the successive trials k and k+1 ($k \geq 1$). Our hypothesis is that the amount of reward obtained at rank k is a major determinant of the selection made at rank k+1. The analysis was separately conducted for trials k in which the animal received a large reward (1.2 ml) and for trials k in which the reward was small (0.4 ml). Two parameters were computed: the proportion of tests in which the animal touched the same target stimulus in trials k and k+1 in the case of large reward in trials k (strategy "large-keep"), and the corresponding proportion in the case of small reward in trials k (strategy "small-keep"). In the repetition period, these two proportions are close to 100%. Indeed, when the animal selects the same target in the successive trials, regardless of the reward (0.4 ml or 1.2 ml) obtained in each trial, he obviously adopts both the "small-keep" and "large-keep" strategies.

The analysis of the SCRs was automated. A SCR was scored when the transient increase in conductance was superior to 0.01 μS and was followed by a slow return to baseline. Frequency of occurrence of the responses within a test (i.e., number of SCRs with respect to number of trials) latency time delay between target touch and SCR onset, rise time from the start of the deflection to the peak, and peak amplitude of each response with respect to the start of the deflection were measured and compared in different tasks: ANOVA (P<0.05) was used if variances were homogeneous and Mann-Whitney U-test (P<0.05) was used if variances were not homogeneous. The homogeneity of variances was studied by the Levene test. SCRs found different with the U-test were also tested using ANCOVA (P<0.05), with RTs and MTs of the arm movements as covariates to remove a possible effect of these parameters. We compared the variability of the times of peaks relative to touch-times (V1) and relative to reward onsets (V2) with a permutation test. We also studied the SCRs amplitude in relation to reward amount. All statistical analyses were performed with Statistica software.

Results

Behavioral results in the TS task

We analyze here a large sample of tests (133 in monkey E, 69 in monkey N) executed during and between the dermal recordings. In the two monkeys, a repetition period could be observed in each test, indicating that the animal always made a decision regarding the best target. Target A was chosen in 96% of tests by monkey E and in 90% of tests by monkey N. Target B was chosen in the other tests. In half of the tests (67 out of 133 in monkey E, 35 out of 69 in monkey N), the evaluation period lasted less than 5 trials in monkey E (Fig. 2a) and less than 10 trials in monkey N. Thus, the selection of the best target was usually more rapid in monkey E (monkey E vs N: $P<9.10^{-4}$). During the search period, the monkey E preferentially touched the left position; monkey N had no clear preference (Fig. 2a). In the repetition period of the corresponding tests, monkey E and monkey N adopted the strategy large-keep in more than 90% of trials. The small-keep strategy, which is correct when the best target is found, was slow to set in (Fig. 2b).

Skin conductance responses

SCRs were recorded in monkey N during 15 sessions, distributed over a period of 9 months and in monkey E during 7 sessions over 3 months.

In monkey N, 5 sessions out of 15 (totaling 42 TS tests and 776 trials), and in monkey E, 2 sessions out of 7 (totaling 95 tests and 449 trials) were finally kept for analysis. The other sessions were discarded primarily because the monkeys did not systematically work in all tasks, in particular in the little-rewarded task C2 and in the non-rewarded task C3.

During performance of the TS trials, SCRs were generated in the two monkeys in relation to the arm movement toward the selected target. They consisted of a transient increase in conductance and were recorded in 85% of trials in monkey N and 75% of trials in monkey E. All the responses had the canonical shape illustrated in Fig. 3. They usually were the only phasic electrodermal event observed during a trial.

Statistical values of SCR parameters are given in Table 1. The data show no evidence that amplitudes of SCRs were influenced by the RTs and MTs of the movements (see the results of ANCOVA in the legends of Figs. 4 and 5) or by the touched position (right vs left; all the differences Z were non-significant at P<.05 in the two monkeys), nor do they show that the SCRs were affected

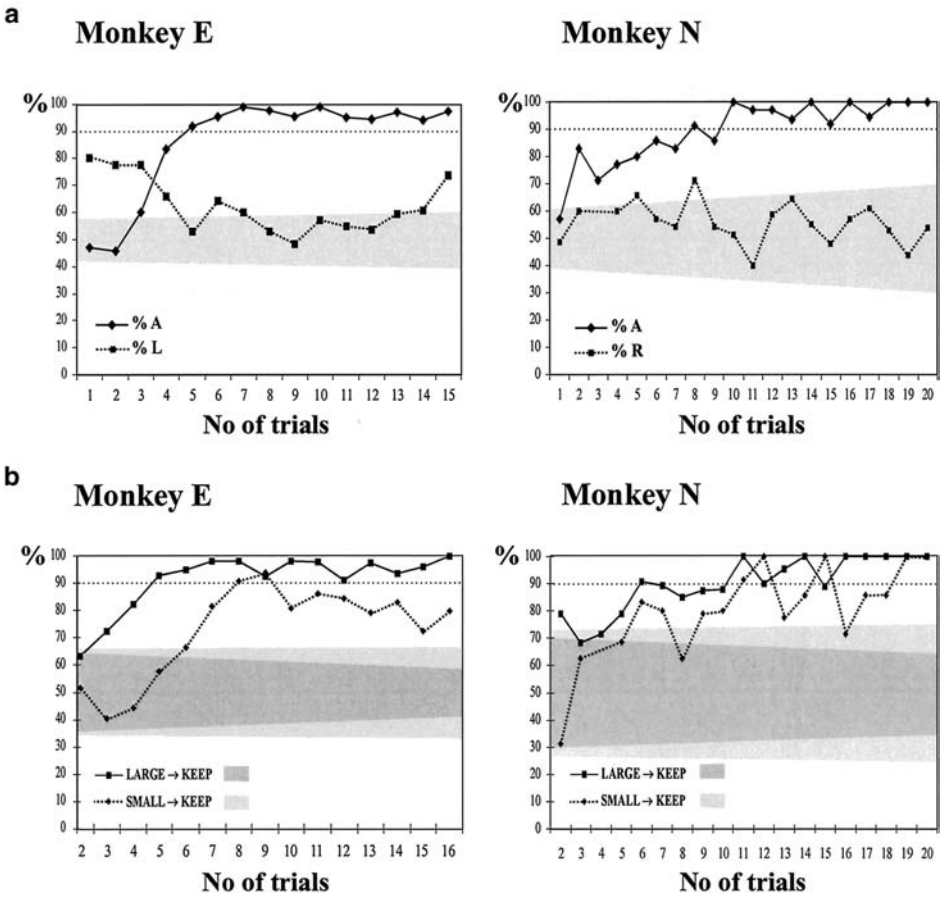


Fig. 2a, b Performance in the TS task. (**a**) Percentage of responses to the best target (*A*) and to the touch position corresponding to the performing hand (left position, *L*, for monkey E, right position, *R*, for monkey N) in the successive trials of selected TS tests. *Shaded areas*, confidence limits (at $P<0.05$) of the null hypothesis (i.e., random behavior, no preferred target; no preferred position). See Results section. (**b**) Percentages of "large-keep" and "small-keep" strategy in successive trials of the same selected TS tests. *Shaded areas*, confidence limits (at $P<0.05$) of the null hypothesis (i.e., random behavior)

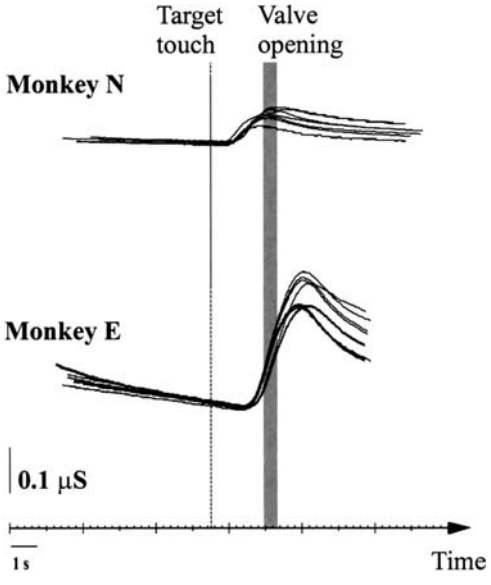


Fig. 3 Examples of skin conductance responses during performance of TS trials

by the reward parameters. In particular, the amplitude of the peaks did not correlate with the quantity of reward (0.4 ml vs 1.2 ml: monkey E, $Z=1.57$, n.s.; monkey N, $Z=-1.94$, n.s.). Similarly, the variability of the times of peak relative to touch-times (V1) was smaller than that relative to reward onset (V2) (monkey N: V2/V1=1.88; V1<V2 at $P<2.10^{-4}$; monkey E: V2/V1=3.33, V1<V2 at $P<4.10^{-8}$). This indicates that the SCRs were more related to the touch-time than to the reward onset.

Table 1 Parameters of skin conductance responses (SCRs) in monkeys E and N in the target-selection task. Data are means ± SD. Units are indicated in parentheses

SCR parameters	Monkey E	Monkey N
Latency (ms)	1,605±506	638±173
Amplitude (μS)	0.23±0.16	0.09±0.06
Rise time (ms)	1,651±395	1,640±777

We further investigated the relationships between SCRs and arm movement in monkey N by altering the time relationship between target-press and reward during one session. The reward was delivered, i.e., the valve was opened, at the time of the press. In the corresponding trials (5 TS tests totaling 70 trials), the SCRs remained identical to those observed with the "normal" TS tasks. In particular, the onset of the response remained time-locked with the target-press with the same average latency.

When the quantity of reward was predictable (tasks C1 and C2), SCRs were observed with the same characteristics as in the TS task (Fig. 4; latencies and rise times not illustrated). This result indicates that knowledge of the

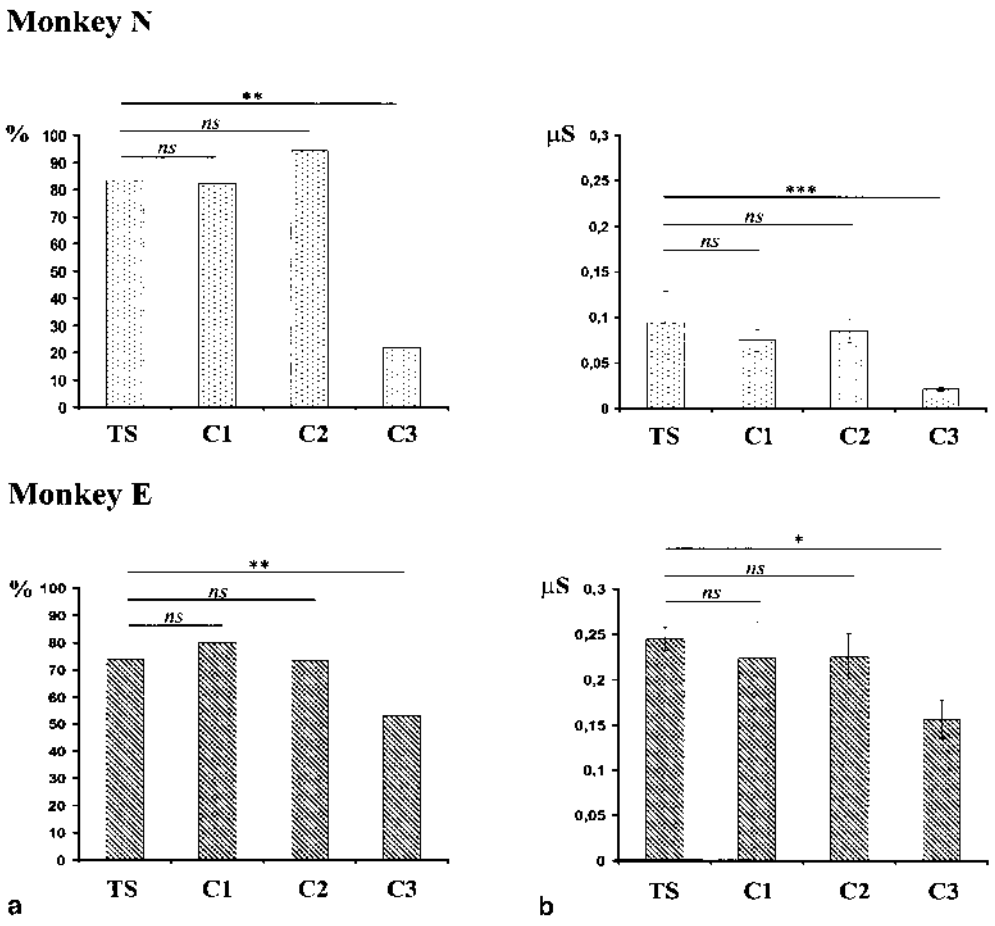


Fig. 4a, b Frequency of occurrence (**a**) and amplitude (**b**) of skin conductance responses (SCRs; mean ± SEM) in the TS task and in the reference tasks C1, C2, and C3 in the two monkeys. Data pooled from 5 sessions in monkey N and from 2 sessions in monkey E. In monkey N, SCRs are similar in all rewarded trials (TS, C1, C2). TS versus C1: frequency, $P<0.30$ (n.s.); amplitude, $Z=-0.48$ (n.s.), TS versus C2: frequency, $P<0.67$ (n.s.); amplitude, $Z=-0.17$, Mann-Whitney *U*-test). In contrast, frequency of occurrence and amplitude of the SCRs are smaller in C3. TS versus C3: frequency, $P<0.01$, amplitude, $Z=10.67$, $P<10^{-6}$; ANCOVA (RTs and MTs as covariates; $F_{1.358}=43.55$, $P<10^{-4}$). In monkey E, SCRs are similar in all rewarded trials (TS, C1, C2). TS versus C1: frequency, $P<0.61$ (n.s.); amplitude $Z=-0,39$ (n.s.). TS versus C2: frequency, $P<0.94$ (n.s.); amplitude, $Z=-0,92$ (n.s.). Frequency of occurrence and amplitude of SCRs are smaller in C3. TS versus C3: frequency, $P<0.01$, amplitude, $Z=2.3$, $P<0.02$; ANCOVA (RTs and MTs as covariates; $F_{1.152}=4.73$, $P<0.03$). *$P<0.05$; **$P<0.01$; ***$P<0.001$

quantity of liquid most likely to be delivered at the end of a trial had no influence on the SCRs. In contrast, when the target-presses were not rewarded task (C3), the SCRs were less frequent and had a smaller amplitude, especially in monkey N (Fig. 4).

The parameters of the SCRs were statistically the same in the evaluation and repetition periods of the TS tasks (Fig. 5, latencies and rise times not illustrated). During the evaluation period, no difference in SCRs was observed in trials in which the animal switched between the targets and those in which no switching occurred (not illustrated).

In the sequence tasks (C4 and C5), the shape of the electrodermal responses depended on the reward schedule (Fig. 6), but not on the succession left → right or right → left of the movements. When the first press yielded no reward and the second press yielded 1.2 ml (task C4), the SCR was generally made of two, sometimes three successive small SCRs. The first response occurred after the first target press (R or L) with the same latency and amplitude as in the TS task and was followed by the other response(s), which occurred without fixed time-relationship with the second target press. The global response culminated after the second touch, approximately at the time of reward delivery. When the first press yielded 1.2 ml and the second yielded 0 ml (task C5), there were in general two successive responses. The first response occurred with the same latency as in the TS task and was immediately followed by another response, evidenced by the inflection point on the rising slope of the global response. The global response culminated well after reward delivery, but before the second touch.

During performance of the correct GO trials of the GO–NOGO task, SCRs analogous to those observed in the TS task were observed. They were rare in the correct NOGO trials and their amplitude was significantly smaller (Fig. 7).

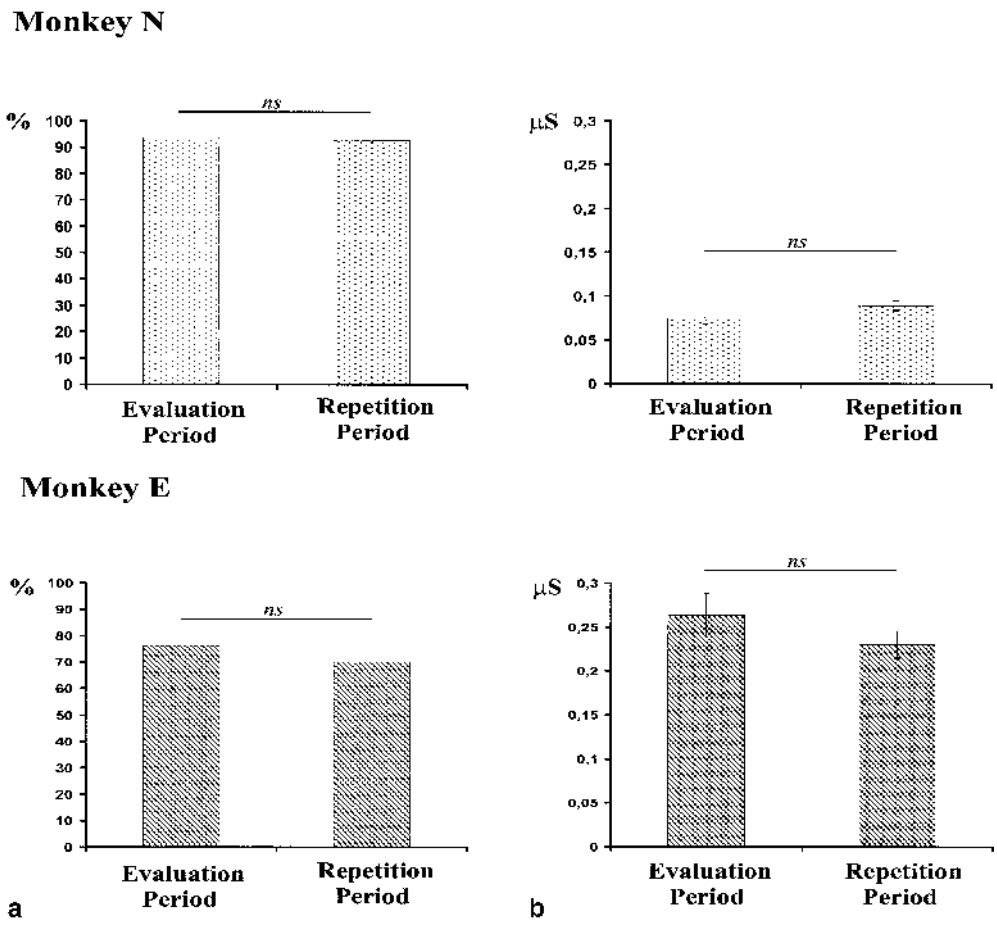


Fig. 5a, b Frequency of occurrence (**a**) and amplitude (**b**) of SCRs (mean ± SEM) during the evaluation and repetition periods of the TS task in the two monkeys (data pooled from 5 sessions in monkey N and 2 in monkey E). These parameters are identical in the two periods. In monkey N, evaluation vs repetition period: frequency, $P<0.439$ (n.s.); amplitude, $F_{1.183}=1.04$ (n.s.). In monkey E, evaluation vs repetition period: frequency, $P<0.747$ (n.s.); amplitude, $F_{1.165}=1.02$ (n.s.)

In the two monkeys, occasional SCRs (in less than 5% of trials) were elicited in relation to the touches of the SP. Their latencies, rise times, and amplitudes were similar to those observed in relation to the target-touches in the TS task. At times, large SCRs, without clear time-relationships to specific event of the trials or specific periods of the tests (evaluation/repetition), were also observed.

SCRs were never observed in relation to cue-onset, execution errors (premature SP release) or free rewards.

Discussion

Based on the performance of rewarded and nonrewarded tests (target-selection, control, GO/NOGO, sequence), we found that conditioned monkeys generate phasic electrodermal responses, time-locked with arm movements toward rewarded targets. These dermal responses could reflect important mechanisms for reward anticipation and consumption.

SCR parameters: interspecies comparisons

The possibility that the recorded signals resulted from a contraction or from a movement of the hand from which skin conductance was measured can be ruled out. The signals studied in this report have the canonical shape of SCRs already described in humans and in animals. When the animal occasionally moved the recorded hand, the resulting signal was generally small, erratic, and never had the smooth profile of the responses illustrated in Fig. 3. These signals were considered as artifacts and rejected.

SCRs with latencies of 1–2 s have been recorded by Levy et al. (1997) at the plantar surface of squirrel monkeys in response to unexpected auditory stimuli. Our shorter latencies might be explained by the fact that SCRs at the upper limbs are shorter than at lower limbs (Shahani et al. 1984) and that the signal responsible for the SCRs may precede the target touch.

SCRs with amplitudes between 0.5 and 0.8 μS (i.e., at least 5 times larger than in the present task) have been recorded in the squirrel monkey by Levy et al. (1997). In humans, SCR amplitudes between 0.01 and 5 μS have been reported (Naveteur et al. 1998).

Parameters of SCRs such as frequency of occurrence, peak-latency, and peak-amplitude were different in the two animals. In humans, interindividual variability in electrodermal parameters (amplitude or latency) have frequently been related to humidity, temperature or thickness of the skin (Fowles and Rosenberry 1973;

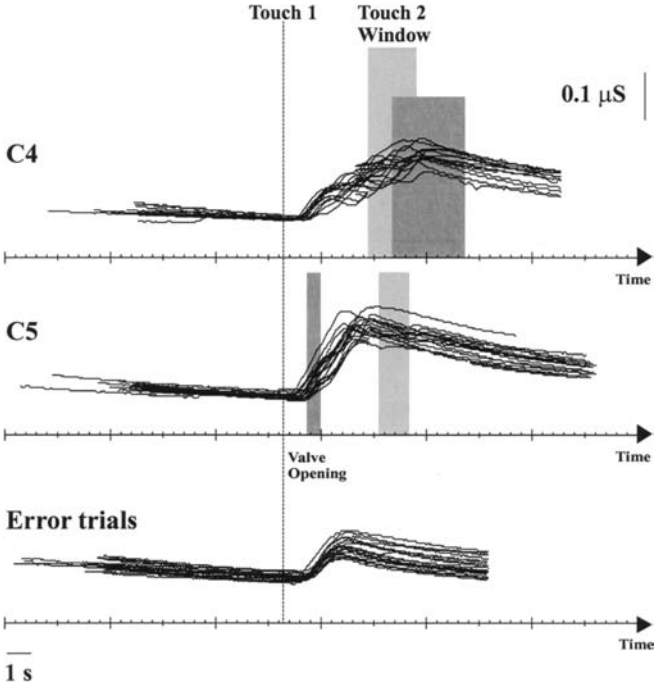


Fig. 6 SCRs in sequential tasks with different reward schedules in monkey N. The SCRs are aligned on the first target touch. In C4, the reward schedule in relation to the first and second touches is 0 ml and 1.2 ml (*upper curves*). In C5, the reward schedule is 1.2 ml and 0 ml (*intermediate curves*). On the time axes, *light gray area*: lower and upper limits of the second target touch; *dark gray area*: lower and upper limits of the valve opening. The *lower curves* correspond to aborted trials due to erroneous selections of the first target. Data pooled from two recording sessions (71 trials). The SCRs are different. C4 versus C5: maximum amplitude, Z=0.39 (n.s.), latencies of the maxima, Z=5.2, $P<10^{-6}$, ANCOVA (RTs and MTs of the second touch as covariates; $F_{2.66}$=27.28, $P<10^{-4}$)

Maulsby and Edelberg 1960; Ba-M'Hamed et al. 1986). These parameters were not measured in our monkeys. In humans, interindividual differences have also been ascribed to central factors linked to the personality (e.g., stabile vs labile subjects; Koelega 1990; Boucsein 1992) and to variability in attending to and processing information (Katkin 1975). Differences between the two monkeys may also be due to methodological aspects which cannot be measured: monkey E had been trained during 24 months before the recording sessions, he worked head-fixed and received a recording chamber; monkey N had been trained during 4 months before the recordings, he worked head-free and had not been implanted.

SCRs and preparation for reward consumption

Our data show a link, not shown before, between electrodermal activity, instrumental action, and reward. Occurrence and onset of the SCRs were tightly related to the execution of arm movements toward the targets. Thus, the SCRs may partly reflect the activation of the corresponding sensorimotor loops. It is well known in humans that SCRs are favored by the execution of movements (Stern and Anschel 1968; Edelberg 1970; Harding and Punzo 1971). Dermal activity modifications seem to index autonomic adjustments associated with specific motor actions (Boucsein 1992). Our data support the claim of several authors that the motor system and the electrodermal control system are closely associated (Darrow 1937; Edelberg 1972, Sequeira et al. 1995; Fredrikson et al. 1998).

Another determinant of SCRs was the anticipation of reward. In monkey N, there was a clear dichotomy between rewarded movements (tasks C1, C2, TS), which were followed by SCRs, and nonrewarded movements in task C3, which were followed by little responses or no responses (Fig. 4). In monkey E, the differences between rewarded and nonrewarded movements were smaller, but were statistically significant. In the two monkeys, movements toward the starting position, which were not directly associated with reward, were rarely followed by SCRs. Our sequence data show that the occurrence and time of onset of SCRs were determined by the reward schedule (Fig. 6). All these data support a crucial role for the reward(s) in the occurrence and organization of SCRs.

The SCRs have the same intensity: (1) in the TS task, in which the amount of reward was not predictable, and (2) in conditions C1 and C2, in which it was predictable. Thus, these anticipatory mechanisms are not sensitive to the amount of reward.

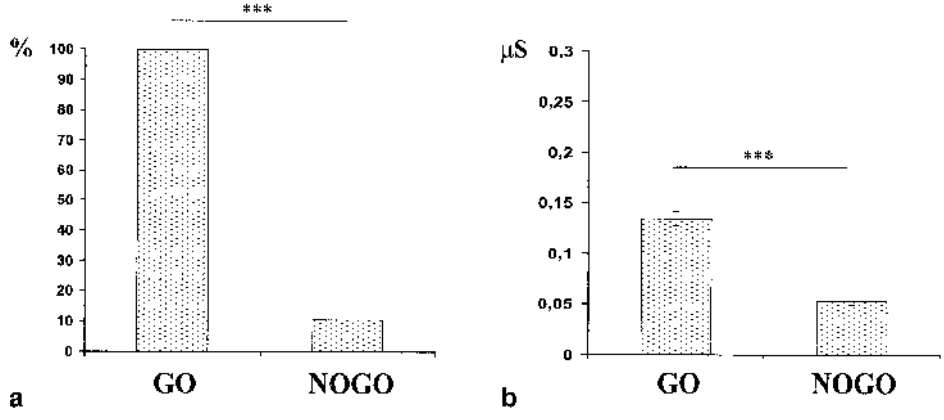


Fig. 7a, b Frequency of occurrence (**a**) and amplitudes (**b**) of SCRs (mean ± SEM) in the rewarded GO and NOGO trials (monkey N). GO versus NOGO: frequency, $P<10^{-4}$; amplitude, Z=7.53, $P<10^{-6}$, Mann-Whitney U-test. ***P<0.001

The fact that the conditioning can tightly associate, in a physiological response, both reward-related and arm movement-related mechanisms has already been observed at the cellular level. In many cells of the striatum (Hollerman et al. 1998, Tremblay et al. 1998), of the parietal cortex (Platt and Glimcher 1999), and of the anterior cingulate cortex (Amiez and Joseph 2000), the motor- or oculomotor-related activity is indexed by the target's reward value. The neuronal mechanisms which associate movement and reward may participate in the genesis of SCRs observed in the present tasks.

According to Panksepp (1982), an expectancy command system, controlled by environmental cues, underlies anticipatory appetitive behaviors. This system resembles the arousal system II that Routtenberg (1968) conceived as a motivational activation system influencing cortical-driven motor actions and preparatory autonomic activity. The neural substrate of this system includes a corticohypothalamic network connected to motor areas via basal ganglia (Boucsein 1992). In the present experiment, due to extensive learning, the visual signals could act as cues labeling the appetitive value of the next movement. As a result, only those movements that predicted the occurrence of a reward were accompanied by an emotional arousal, revealed by SCRs. Finally, when related to the arousal dimension of approaching behaviors discussed by Damasio (1994), SCRs would mark the changes of the internal state of the organism in anticipation of reward consumption.

SCRs and detection of the best target

We found that the SCRs occurred *after* the target touch. They were identical in the evaluation and repetition periods of the TS task and in the rewarded control tasks. This indicates that the neuronal networks at the origin of the SCRs have no particular role in the cognitive processes (working memory, response monitoring, selective attention, set shifting, etc.) that are presumably associated with the detection of the best target.

Although there is no direct evidence of an equivalence between the two tasks, it might be interesting to compare the present results with those obtained in the Iowa gambling task (Bechara et al. 1994, 1996), which shares with the TS task many formal similarities. In the gambling task, SCRs occurred *before* the card selection and showed marked variations of amplitude according to the different stages of the discovery and knowledge of the task. When its contingencies were better known by the subjects, the anticipatory SCRs tended to disappear (Bechara 2001). We conclude that the anticipatory dermal activity observed in humans in relation to decision-making tasks is *not* observed in animals performing the TS task.

Two explanations, not exclusive from each other, may account for this difference. One is the risk. For Critchley et al. (2001) and Bechara et al. (1996, 1997, 1999), the notion of risk is central to the occurrence and interpretation of the anticipatory SCRs. In the TS task, the risk is minimal. Whatever the choice, the animal is rewarded. Another explanation is the conditioning and the familiarity with the task. In the gambling task, the subjects discover a novel environment and a novel task. In the TS task, the environment is familiar and the task is well mastered, as revealed by the procedure adopted by the animal (the delayed use of the large-keep strategy) and by the rapid detection of the best target. One hypothesis is that the animal is in a situation of cost-benefit analysis, which is not accompanied in humans by the activation of emotional (somatic) markers (Damasio 1994). Familiarity with the task may also explain the lack of dermal responses to errors (selection errors in the GO-NOGO task, execution errors due to early SP release in all tasks). The animal may not react emotionally to errors that have been committed many times and that have become an integral part of his performance.

Our results nevertheless suggest that the SCR technique has the potential for revealing direct links between decision processes in monkeys and in humans, lending credence to the monkey as a neurophysiological model of decision-making. This demonstration will require specific conditions such as placing the animal in unfamiliar situations in which decisions may have aversive consequences.

Acknowledgements We thank M.L. Loyalle for technical assistance, and K. Knoblauch and G. Cousens for helpful comments on the manuscript. This work was supported by Ministère Delégué de la Recherche, ACI 2002.

References

Amiez C, Joseph JP (2000) Decision making in the monkey: behavioral and neural data. Abstr Soc Neurosci 749.7

Ba-M'Hamed B, Ciancia F, Delerm B, Roy JC, Sequeira-Martinho AH (1986) Influence of skin temperature on latency and amplitude of skin potential responses in the cat. Biol Psychol 22:59–67

Bechara A (2001) Neurobiology of decision-making: risk and reward. Semin Clin Neuropsychiatry 6:205–216

Bechara A, Damasio AR, Damasio H, Anderson SW (1994) Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 50:7–15

Bechara A, Tranel D, Damasio H, Damasio AR (1996) Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. Cereb Cortex 6:215–225

Bechara A, Damasio H, Tranel D, Damasio AR (1997) Deciding advantageously before knowing the advantageous strategy. Science 275:1293–1295

Bechara A, Damasio H, Damasio AR, Lee GP (1999) Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. J Neurosci 19:5473–5481

Boucsein W (1992) Electrodermal activity. Plenum, New York

Critchley HD, Mathias CJ, Dolan RJ (2001) Neural activity in the human brain relating to uncertainty and arousal during anticipation. Neuron 29:537–545

Culp WC, Edelberg R (1966) Regional response specificity in the electrodermal reflex. Percept Mot Skills 23:623–627

Damasio AR (1994) Descartes' error. Emotion, reason, and the human brain. Putnam Books, New York

Darrow CW (1937) Neural mechanisms controlling the palmar galvanic skin reflex and palmar sweating. Arch Neurol Psychiatry 37:641–663
Edelberg R (1970) The information content of the recovery limb of the electrodermal response. Psychophysiology 6:527–539
Edelberg R (1972) Electrodermal recovery rate, goal-orientation, and aversion. Psychophysiology 9:512–520
Fowles DC, Rosenberry R (1973) Effects of epidermal hydration of skin potential responses and levels. Psychophysiology 10:601–611
Fowles DC, Christie MJ, Edelberg R, Grings WW, Lykken DT, Venables PH (1981) Publication recommendations for electrodermal measurements. Psychophysiology 18:232–239
Fredrikson M, Furmark T, Olsson MT, Fisher H, Andersson J, Langström B (1998) Functional neuroanatomical correlates of electrodermal activity, a positron emission tomographic study. Psychophysiology 35:179–185
Harding G, Punzo F (1971) Response uncertainty and skin conductance. J Exp Psychol 88:265–272
Hollerman JR, Schultz W (1998) Dopamine neurons report an error in the temporal prediction of reward during learning, Nat Neurosci 1:304–309
Katkin ES (1975) Electrodermal lability: a psychophysiological analysis of individual differences in response to stress. In: Spielberger CD, IG Sarason (eds) Stress and anxiety, Vol 2. Wiley and Sons, Washington, pp 141–176
Koelega HS (1990) Vigilance performance, a review of electrodermal predictors. Percept Mot Skills 70:1011–1029
Levy JK, Igarashi M, Ledet JC (1997) Electrodermal response in the squirrel monkey. Percept Mot Skills 45:943–948
Maulsby RL, Edelberg R (1960) The interrelationship between the galvanic skin response, basal resistance and temperature. J Comp Physiol Psychol 53:475–479
Naveteur J, Godefroy O, Sequeira H (1998) Electrodermal level asymmetry in a unilateral brain-damaged patient. Int J Psychophysiol 29:237–245
Panksepp J (1982) Toward a general psychobiological theory of emotions. Behav Brain Sci 5:407–467
Platt ML, Glimcher PW (1999) Neural correlate of decision variables in parietal cortex. Science 100:233–238
Pribram KH, McGuinness D (1975) Arousal, activation, and effort in the control of attention. Psychol Rev 82:116–149
Routtenberg A (1968) The two-arousal hypothesis: reticular formation and limbic system. Psychol Rev 75: 51–80
Sequeira H, Ba-M'Hamed S, Roy JC (1995) Fronto-parietal control of the electrodermal activity. J Autonom Nerv Syst 53:103–114
Shahani B, Halperin JJ, Boulu P, Cohen J (1984) Sympathetic skin response-a method of assessing unmyelinated axon dysfunction in peripheral neuropathies. J Neurol Neurosurg Psychiatry 47:525–536
Siddle DAT, O'Gorman JG, Wood L (1979) Effects of electrodermal lability and stimulus significance on electrodermal response amplitude to stimulus change. Psychophysiology 16:520–527
Stern RM, Anschel C (1968) Deep inspirations as stimuli for responses of the autonomic nervous system. Psychophysiology 5:132–134
Tremblay L, Hollerman JR, Schultz W (1998) Modifications of reward expectation-related neuronal activity during learning in primate striatum. J Neurophysiol 80:964–977