Bilateral Processing of Motor Commands in the Motor Cortex of the Cat During Target-Reaching

S. Perfiliev

Department of Physiology, The Sahlgrenska Academy at Göteborg University, Göteborg, Sweden and Institute of Physiology, St. Petersburg State University, St. Petersburg, Russian Federation

Submitted 28 July 2003; accepted in final form 7 December 2004

Perfiliev, S. Bilateral processing of motor commands in the motor cortex of the cat during target-reaching. J Neurophysiol 93: 2489–2506, 2005. First published December 15, 2004; doi:10.1152/jn.00720.2003. Single-unit activity of the motor cortex (area 4γ) was studied in cats performing reaching with the contra- versus ipsilateral forelimb. Reaching was initiated by a tone burst (Go cue), different limbs were used in separate blocks of trials. During reaching performed with the contralateral limb, three types of neurons were observed. The first type had biphasic pattern with an initial component locked to the Go cue followed by a component locked to the onset of reaching. The second type of neurons had monophasic discharges correlated both with the onset of the stimulus and with the movement. The third type showed responses related to the movement. Activity of the same cells investigated during reaching performed with the ipsilateral limb revealed that the cue-locked responses of the cells of the first type were effector independent, i.e., similar discharges locked to the Go cue were generated. The movement-related component of these cells was drastically reduced. The activity of some cells of the second type was suppressed during reaching with the ipsilateral limb. When performance was switched between limbs, a significant change of background discharge frequency was observed in 31% of the cells. The present results suggest that the sensory cue triggers elaboration of motor commands for reaching in both motor cortices, but further sensorimotor transformation is completed in only one hemisphere but is aborted actively in the other. It is also suggested that a certain pattern of background activity may serve a tuning function for elaboration of the command in the proper hemisphere.

INTRODUCTION

Activation of ipsilateral motor cortical areas during preparation and execution of a unilateral motor response has been documented in electrophysiological (Deecke et al. 1969; Salmelin et al. 1995) and imaging studies (Cramer et al. 1999; Kobayashi et al. 2003; Roland 1984; Roland et al. 1980). Yet neither the neurophysiological mechanisms nor the functional significance of this finding are clear. Bilateral activation of nonprimary motor cortical areas can contribute to the programming of a unilateral movement. On the contrary, coactivation of the primary motor cortical areas may cause undesirable involuntary mirror movements on the opposite side of the body (Kristeva et al. 1991; Mayston et al. 1999) that, most likely, serve no function but rather reflect interhemispheric interaction during a unilateral response. It has been observed that undesirable coactivation, expressed as mirror activity, increases with the complexity of the unilateral task (Salmelin et al. 1995), when generating high levels of force (Dettmers et al. 1996), when the subjects are in state of fatigue (Zijdewind and Kornell 2001), during recovery after stroke (Cramer et al. 1997), and in young children (Reitz and Muller 1998). All these effects may have been caused by an imbalance between the excitatory and the inhibitory interhemispheric interactions, shown to be potently employed during unilateral tasks (Calford and Tweedale 1990; Clarey et al. 1996; Kogan et al. 1978). The possibility of nonfunctional activation of the ipsilateral cortex is also suggested by the observation that it occurs more often during performance with the nondominant, i.e., less skillful hand (cf. Kobayashi 2003), indicating that it is not required for a well-established unilateral response. It is therefore an important issue to what extent an observed ipsilateral cortical activity serves direct function during unilateral motor response rather than being an undesirable effect originating from the complexity of the interhemispheric interaction.

Only few studies with single-unit recording in the ipsilateral cortex focus on the problem of interhemispheric relationships. Weak activity during movements with the ipsilateral limb was found in the primary motor cortex of monkey supposedly related to a small number of uncrossed corticospinal fibers or to the control of trunk and proximal limb muscles (Matsunami and Hamanda 1978, 1981). However, in the premotor cortex, many cells show similar activity time locked to the sensory signal during ipsi- and contralateral movements (Brinkman and Porter 1979; Cisek et al. 2003; Rizzolatti et al. 1987; Tanji et al. 1988). Several studies, focusing on bimanual coordination have shown activity in the MI area of the monkey during ipsilateral movements and it has been suggested that it is related to the coordination of the two limbs in bimanual tasks (Cardozo de Oliveira et al. 2001; Donchin et al. 1998, 1999, 2002; Steinberg et al. 2002). Recently effector-independent activity was observed in the dorsal premotor cortex during ipsi- and contralateral movement performed in separate block of trials (Cisek et al. 2003).

Both anatomically and functionally, the motor cortex of the cat is less subdivided into separate areas than the monkey cortex. It has previously been shown that activity locked to the sensory cue, encoding more abstract parameters of the motor task, and activity related to the execution of the movement can be observed within the same area and even, to some extent, in the same neuron (Cherenkova et al. 1992; Perfiliev 1998). Taking advantage of this simplicity, the sensory- and movement-related activity in the ipsi- and contralateral motor cortices were investigated in the present study by comparing the
response patterns of motor cortical cells when reaching movements were performed with the contra- versus ipsilateral limb. It will be shown that in the cat motor cortex the cue-locked activity is effector independent, i.e., short-latency responses look alike regardless of the forepaw used. Second, some neurons related to preparation of the movement showed reciprocal responses during ipsi- versus contralateral reaching, i.e., excitatory responses during reaching with the contralateral limb but short-latency suppression during reaching with the ipsilateral one. It is suggested that a Go signal for a unilateral movement, besides initiation of the motor command in the contralateral cortex, simultaneously triggers a mirror command in the opposite hemisphere, but further processing in the ipsilateral cortex is actively inhibited. It is also suggested that the undesirable mirror movements observed in humans may be caused by a deficit in active suppression of the mirror command in the ipsilateral cortex. Some of these results have been published previously in abstract form (Perfiliev 2000).

METHODS

Behavioral tasks

The experiments were performed on six adult male cats. The animals were unrestrained, sitting comfortably in front of a wall with a hole through which a tray (20 × 50 mm) with a morsel of meat could be inserted. The sitting position was chosen to avoid early postural adjustments observed in cats performing reaching in the standing position (Birjukova et al. 1989; Schepsens and Drew 2003). The cats were trained to perform a target-reaching movement to the tray and retrieve the food after the onset of the Go signal; this is illustrated in Fig. 1A. The Go signal was a tone burst (1.8 kHz, 75 dB, duration: 100 ms, rising and falling phases: 10 ms) from a speaker positioned behind the wall in the midline. In the first test, denoted “fast task,” the tray appeared 500 ms after the Go cue and was presented during a limited time period (250–400 ms) so that the cats were required to initiate the movement before the appearance of the tray. In the second, “slow task” without time constraints, a small platform (not illustrated) was fixed 2 cm below the hole through which the tray was inserted. When the Go signal was presented, the animal had to make a reaching movement to the platform and put forelimb on it, the tray was then inserted. The endpoint of reaching in a slow task was, therefore, 2 cm lower and 2 cm closer to the cat compared with the fast task. The fast task was characterized by more robust neuronal responses and was useful for estimating the basic firing pattern and for dividing the cells into different types. The slow task, in which the investigated events were rather separated in time, was more effective for determining whether discharges were related to the Go cue or to the movement. Depending on the individual preference of the cat and on the purpose of the experiments one of the tasks could be used more often.

Two animals (NN 1 and 2) were trained to perform the task with the left limb throughout all experiments; the other four performed reaching movements with either forelimb in separate blocks of trials (in 1 of 4 cats, the transfer of the task to another limb was done after implantation of the electrodes). Each block included 25–100 trials, each daily session could include three to five identical blocks. The

FIG. 1. A: schematic drawing of the cat during experiment. ≡, the source of the Go signals. B: summary of the recording sites in all cats. ○, the points of implantation of the bundles. C: examples of typical electromyographic (EMG) patterns during “fast” and “slow tasks.” Biceps EMG of the limb performing reaching (contra) and triceps EMG of the opposite limb (ipsi) are shown.
forelimb with which the session started varied from day to day. To switch the performance between the forelimbs, a soft leather sock was put on the paw which should not be used. The onset of the movement was defined as time an electrical contact between the limb and the floor was broken. In some sessions, the end of the reaching movement was recorded by photodiodes positioned at the edge of the hole through which tray was inserted.

In one of four cats trained with either limb, occasionally, two different Go cues were used: for one limb, a tone burst and for the other, a simultaneous presentation of a click and a light flash. It has previously been shown that sensory stimuli of different modalities and/or with different physical parameters generate virtually similar neuronal sensory responses in different motorcortical areas (Lamarre et al. 1983; Perfiliev 1994; Tanji and Kurata 1982). In the motor cortex of the cat, the difference may at most be a slight change of response latency and frequency of the initial phase (“click + light”) generates responses with slightly shorter latency and more higher frequency during 1st 20 ms compare with the response generated by the “tone burst”) (Perfiliev 1994). Therefore the neuronal response patterns during reaching movements with the ipsi- and contralateral limb, can to some extent be compared also when different cues were used for the two limbs. In a preliminary study, sensory responses to the Go cue were observed in the motor cortex during movements with the ipsilateral limb (Perfiliev 1995). To exclude the possibility that such responses were due to the fact that the cats were trained to perform the movement with either limb (i.e., that both hemispheres were conditioned to the same signal), ipsilateral activity was studied in one cat trained, in the present experiments, to perform reaching with left limb only, i.e., the left motor cortex was never conditioned to respond with a movement to the stimulus. The task was then transferred to the other limb during neuronal recording.

Electrodes

Highly flexible hair-like electrodes based on thin silver glass-coated wires were used. The external diameter of the electrodes was 45–55 μm, and the diameter of the silver wire inside 6–8 μm (electrode impedance; 1–2.5 MΩ measured at 1 kHz). Three to five electrodes were assembled into the bundle positioned in a miniature micromanipulator that was fixed on the skull during the surgery. Details of this technique have been published previously (Cherenkova et al. 1987).

Surgery

The animals were anesthetized with sodium-pentobarbital (40 mg/kg). A 3-mm-wide opening was made in the bone over the lateral part of the anterior sigmoid gyrus which corresponds to the distal representation of the forelimb. The dura mater was removed and a plastic cap was fixed to the opening by dental acrylic. A guiding tube (1.2 mm diam) containing the electrode bundle, was inserted into a hole in the cap. The cap and guiding tube were covered by dental acrylic, which was also used to fix the micromanipulator and the connector on the vertex. After the installation, the bundle was advanced into the cortex and the electrodes connected to an amplifier to verify that unit activity could be recorded.

In two cats, silver monopolar electrodes were implanted into the biceps and triceps muscles (medial head) for recording of EMG activity. The electrodes were connected to a socket on the skull via thin subcutaneous stainless steel wires.

Data collection and analysis

Thin, flexible electrodes permanently implanted into the cortex allow stable recording of single neurons during 2–3 mo. The signals from the microelectrodes were amplified 10 times by a preamplifier close to the socket on the skull and filtered with a band-pass filter (0.2–10 kHz). The EMG signals were filtered at 0.2–1 kHz. After further amplification, all signals were recorded on analogue tapes. The action potentials of individual cells were discriminated with a two-window amplitude discriminator, sampled at 10 kHz, and transferred to a computer. As control of the discrimination, the distribution of the spikes amplitude was used.

The latencies of the neuronal responses were measured in cumulative peristimulus time histograms (PSTH; 5- or 10-ms bin width, the number of cumulated trials ranged from 30 to 70). The onset of a response was defined as the bin with a number of spikes below or above 2 SD of the average number of spikes per bin during 700 ms of prestimulus period. The onset of the response in individual trials was determined on rasters plotted with high time resolution and was defined as the middle of the inter-spike interval that was half or less than the average prestimulus interspike interval, provided that the length of at least two immediately after interspike intervals was the same or shorter.

To make a preliminary division of the neurons into the groups, the temporal relation of the neuronal discharges with the stimulus and with the movement was appreciated by comparing raster plots aligned at the Go cue with those aligned at the onset of the movement. 100 cells which in most trials showed comparably clear change points of the interspike intervals were selected for determination of the response latencies in individual trials and for further calculations of coefficients of correlations and regression analysis. Approximately equal number of cells was selected from each preliminary defined group. The methods described by Lamarre et al. (1983) and Vicario et al. (1983) were used for quantitative estimation of the relationship between the events and the neuronal responses. The lead time, i.e., the time by which the neuronal response leads the onset of the movement, was plotted against the reaction time. A plot was also made of the response latency, defined as the time between the stimulus onset and the beginning of the response, against the reaction time. A response time-locked to the sensory cue would result in a high correlation between the lead times and the reaction times as well as a least square regression line with a slope close to 1. On the contrary, there would be no significant correlation between the response latencies and the reaction times. The opposite results would be expected for responses correlated to the onset of the movement. Standard statistical tests were used for describing relationships between variables or for comparing groups (Spearman rank, regression analysis, paired t-test). STATGRAPHICS and ANOVA software packages were used.

The somatic receptive fields of all recorded neurons were tested by palpation and during passive movements of the limb induced by the experimenter. At the end of the experiments microstimulation (330 Hz, 40–100 biphasic pulse, each phase 0.2 ms, 30–100 μA) was applied through the recording electrodes for identification of recording sites. Then the electrodes were surgically removed and the sites of the penetrations were inspected visually.

The experiments were conducted in accordance with the National Institutes of Health guidelines on care and use of animals in research.

RESULTS

Reaching with the contralateral limb

REACTION TIME AND EMG ACTIVITY. Parameters characterizing the performance were analyzed in four cats (NN 1–NN 4) during reaching with the left limb. The fast task was performed with a success rate of 60–80%. During unsuccessful trials, the reaching movement was completed but was too late to grasp the reward in time. A stable and fast performance with mean reaction times of 520 ± 76, 370 ± 39, 448 ± 55, and 433 ± 53 (SD) ms for the different cats, was observed during 30–80 trials. The movement times ranged for all four cats from 270 to 460 ms. The rather long reaction time of the first cat is explained by his persisting attempt to delay the onset of
movement and to start it simultaneously with presentation of the tray with food. Toward the end of the sessions, all animals could have reaction times of ~700–800 ms that could be caused by decreased motivation and fatigue. In the slow task, the animals performed ≤200 trials but with very variable movement parameters during the second part of the session; reaction time could exceed 1,000 ms and movements time ranged from 290 to 850 ms.

The pattern of EMG activity recorded from the biceps and triceps muscles of both limbs was rather similar from session to session but different during the fast and the slow tasks especially if one of the tasks was used only occasionally. This is illustrated in Fig. 1C. During the fast task, the EMG activity of the biceps of the acting limb was leading the onset of the movement by 40–60 ms (peak activity at 20 ms) and decreased ~100 ms after the onset of the movement. In contrast, a rather continuous activation of the biceps throughout the movement starting usually 70–170 ms before the lift-off was typical for the slow task. Nevertheless, if both tasks were used regularly in the same cat, the EMG pattern of the biceps became intermediate and rather similar during both tasks, i.e., the first phasic response was followed by a less potent continuous activation. Often, during fast task, the EMG activity of the supporting limb did not lead activation of the limb performing reaching and was usually not observed before the onset of the movement, indicating that in many trials postural adjustments were made in advance. In some trials, a small phasic response could be observed ~20 ms before the lift-off, i.e., after the gross phasic activation of the limb used for reaching. The EMG activity in muscles of the supporting limb observed during the slow task indicated that the postural adjustments varied from trial to trial. Muscles of the supporting limb were usually activated slightly ahead of those of the limb performing the task, although in several trials the muscles of the performing limb were activated first. Recent findings in the cat performing reaching in sitting position showed that first change of force are often observed at platforms supporting the hindlimbs, indicating that hindlimb muscles are activated first (Sasaki S and Naito K, unpublished observation). Table 1 shows average time of muscle activation relative to the onset of the movement in two cats. Importantly, even during trials made with reaction times ranging from 700 to 1,000 ms, EMG activity in any of the recorded muscles of any limb did not lead the onset of the movement by >200 ms. In contrast to the results of Schepens and Drew (2003) in the cat performing reaching in standing position, a temporal decoupling of the EMG activity related to the postural adjustments from that related to the lift-off was not found in the present experiments.

**Neuronal database**

All electrode implantations in the present study were located in the lateral part of the anterior sigmoid gyrus (Fig. 1B) which projects monosynaptically to the C3–C4 propriospinal neurons (Alstermark and Ohlson 2000) known to mediate the command for reaching movements (cf. Alstermark and Lundberg 1992). Microstimulation evoked contractions of the forelimb muscles or, at high stimulation strength, lifting of the forelimb. The receptive fields of the majority of the cells recorded from were located on forelimb. This indicates that the observed task-dependent activity should be related to the control of the forelimb. It should nevertheless be considered that due to the method used for recording, the population data may have a certain degree of bias. A permanently implanted bundle of flexible electrodes allows daily tracking during ≤3 mo without noticeable decrease of the activity in the area of implantation. Neurons with new response properties can be observed throughout this period, presumably due to the high flexibility of the electrodes. On the other hand, in about a month and half, cells with identical response patterns can be found regularly, suggesting recording of the same cells. Although the cells with clearly identical responses were excluded from the population analysis, some degree of repetition of the collected data are possible.

Three hundred fifty neurons with task-related activity during reaching performed with the contralateral limb were recorded in the cats NN 1–NN 4, 271 cells were selected for further analysis. The group of discarded neurons included 33 cells demonstrating inhibitory modulation during the task and 35 with increasing discharge frequency at the onset of the movement or later. Eleven cells were excluded from analysis due to weak and irregular responses. Except for two neurons (cf. Fig. 4B) the basic structure of the neuronal response pattern was similar during fast and slow tasks in all cells. In the slow task, the duration of the response was usually prolonged and the discharge frequency was slightly decreased.

If identifiable, the receptive fields of the cells were mostly located around the elbow and shoulder, more rarely on the wrist or distal pads.

**Responses patterns during reaching with the contralateral limb**

The modulation of firing frequency initiated before the onset of the reaching and that could therefore be safely attributed to a feed-forward command rather then to a reafferent signal was considered for classification. The cells were subdivided into different types depending on: the number of components in the response pattern initiated before the onset of the movement, the value of the response latency, and the correlation of the discharges with the Go signal versus the onset of the movement. The cells were classified into three major groups: neurons with complex response pattern, neurons with a sensori-motor response, and neurons with a motor response. A response pattern typical for each group is presented in perievent histograms in Fig. 2 that are aligned with the onset of the Go cue (left) or with the onset of the movement (right).

<table>
<thead>
<tr>
<th>Cat, Muscle</th>
<th>Fast Task</th>
<th>Slow Task</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat III 1B</td>
<td>−47 ± 6</td>
<td>−147 ± 11</td>
</tr>
<tr>
<td>lTr</td>
<td>not active</td>
<td>not active</td>
</tr>
<tr>
<td>rTr</td>
<td>−11 ± 13</td>
<td>−159 ± 14</td>
</tr>
<tr>
<td>Cat IV 1B</td>
<td>−27 ± 4</td>
<td>−50 ± 13</td>
</tr>
<tr>
<td>lTr</td>
<td>−23 ± 5</td>
<td>−48 ± 14</td>
</tr>
<tr>
<td>rTr</td>
<td>7 ± 6</td>
<td>−37 ± 30</td>
</tr>
<tr>
<td>rTr</td>
<td>6 ± 6</td>
<td>−40 ± 31</td>
</tr>
</tbody>
</table>

All values (means ± SD) are given relative to the lift-off of the reaching limb. B, biceps; Tr, triceps (medial head); l, left limb (reaching); r, right limb (supporting); EMG, electromyographic.
NEURONS WITH COMPLEX RESPONSE PATTERN. This group is represented by the neuron in Fig. 2A and includes 43 (12%) cells with response patterns consisting of two components both initiated before the onset of reaching. As can be seen in the histograms in Fig. 2A aligned with the onset of the cue, the cell shows an initial short-latency response and a more powerful later phase. When aligned with the onset of the movement a clearly different pattern emerges, the first component is dissipated and the second increased. To assess these changes quantitatively, the mean number of spikes at the peak of the movement-related components were compared. Two bins with highest number of spikes were selected from the movement-related component in each PSTH. The increase of second component was statistically significant \((P < 0.005)\) and ranged for all cells from 19 to 36%. Such a change of pattern was used as criteria for a biphasic response pattern. The peak frequency of the first component for all cells ranged from 25 to 65 Hz, whereas the range of peak frequency of the second component was 100 to 300 Hz. In all cells, the latency of the first component ranged from 20 to 110 ms (66 ± 22).

NEURONS WITH SENSORIMOTOR RESPONSE. The response of these cells had only one component initiated before the onset of the movement. A typical cell is presented in Fig. 2B. The response latency is \(\sim 170\) ms. The slight (0.5%) increase of the response when the histogram was align with the onset of the movement was not statistically significant \((P = 0.22)\), suggesting that it correlates with the onset of the sensory cue as well as with the onset of the movement. Such type of response was found in 186 cells and with latencies ranging from 170 to 300 ms (228 ± 34). The criterion for attributing a cell to this group

---

**FIG. 2.** The 3 most typical discharge patterns obtained from 3 different neurons (A–C) during fast task presented as peristimulus time histograms (PSTH). All histograms (bin width: 40 ms) on the left are synchronized at the onset of the Go stimulus (a). Histograms on the right are synchronized at the onset of the movement. Short horizontal lines below the PSTH indicate the range of movement onset in different trials. The number of cumulated trials \((n)\) and response latency (RL) is indicated for each PSTH. Note that while all cells have a well-developed component related to the onset of the movement, their responses to the sensory cue are clearly different.
was a significant correlation of the discharges with both the Go cue as well as with the onset of the movement (see following text).

**NEURONS WITH MOTOR RESPONSE.** Forty-two (12%) cells showed discharges strongly related to the onset of the movement as illustrated in Fig. 2C. Typically, powerful discharges developed within 100–200 ms prior to the movement with the peak frequency located within 100 ms after the onset of the movement. The cells in this group showed the highest peak discharge frequencies (compare the number of cumulated trails for each PSTH in Fig. 2), which could exceed 300 Hz. The response latency of these cells ranged from 200 to 400 ms (296 ± 45 could be even more in case of exceptionally long reaction times). For all cells of this group, the mean number of spikes at the peak of the movement-related component was 22–57% ($P < 0.005$) higher in PSTHs aligned with the onset of the movement than in PSTHs aligned with onset of the cue. The major part of these cells showed response latency in the same order as the previous type, but, as it will be shown below, the absence or very low correlation with the cue made this group distinguishably different.

Further, the correlation of the neuronal responses with the onset of the Go cue and with the onset of the movement was investigated for each group. This is illustrated in Fig. 3, which shows the discharge pattern of three cells representing different groups in raster plots. The first component of all cells with biphasic pattern, represented by cell A in Fig. 3, showed high correlation with the cue ($r$ and slope $>0.7$) but low or no correlation with the onset of the movement ($r < 0.5$, slope $<0.3$). Accordingly, this component represents a sensory response. In cell A, the second component of the response pattern is fused with the first one and could be better identified in PSTHs. Nevertheless, in many cells it could be clearly seen in individual trials as a drastic increase of the discharge frequency before lift-off and locked to the onset of the movement.

The discharges of the group with sensorimotor pattern, represented by the cell in Fig. 3B were well correlated with the sensory cue as well as with the onset of reaching. In some trials in the raster plot aligned at the time of lift-off, two points of change of the interspike intervals can be identified, although not very clearly (observe trials 2–6 from the bottom). This may suggest that a residual and degraded sensory response is present in these trials. Similar discharges were occasionally observed in some cells of this type, nevertheless they never appeared as a clear sensory response like in the cells of the first type.

The responses of the cells of third group showed high values of the coefficient of correlation and of the slope of the linear regression between response latency and reaction time, indicating that the response was movement-locked (Fig. 3C). In a few cells, a significant correlation with the Go cue was observed but with very low coefficient of linear regression (slope: $<0.2$). Responses with latencies exceeding 300 ms had no correlation with the onset of the Go cue.

The cells with complex response pattern and neurons with motor responses had clear and stable receptive fields located usually within one segment of the forelimb, i.e., on the wrist, elbow, or shoulder. They could be activated by slight touch, deep palpation, or by passive movement around the elbow or the shoulder joint. The neurons with sensorimotor type had large receptive fields, including the elbow and shoulder segments and usually responded to deep palpation of the muscles. The responses were often weak and the exact border of the receptive field was difficult to determine. In many cells (60%), receptive fields could not be identified.

Further analysis of the neurons with complex response pattern revealed that depending on the timing of the movement-related component the cells of this group could be divided in two subtypes which are shown in Fig. 4. Both neurons have clear cue-locked responses with a latency of 30 ms for cell in A and 70 ms for cell in B. The well-separating movement-related component of the cell in A leads the onset of the movement by ~120 ms and its high frequency is sustained during lift-off and for ~100 ms afterward with the peak discharge frequency at the onset of the movement. On the contrary, the movement locked response of cell B develops ~200 ms before the onset of the movement (cf. the lower part of the raster plot that shows trials with longer reaction times) and ceases abruptly in most of the trials when the movement is initiated. Therefore the features of this cell were time of peak discharge frequency before lift-off and drastic decrease of the response thereafter. These differences in timing of the movement-related components were used as a criteria to divide these cells into two different subtypes, which will be referred to as biphasic-a and biphasic-b, respectively. In addition, it was also found that during the slow task, the biphasic-b type cells may have a third component of the response developing after the onset of the reaching movement. This is shown in Fig. 4B2 (the latest and most pronounced response is caused by the movement from the platform to the food-box). The fact that a third component is not present during the fast task suggests that it is a reafferent signal (nevertheless, in some biphasic-b cells the third component was present also during the fast task). Palpation around the elbow joint suppressed the activity of the biphasic-a cell. The biphasic-b cell could be activated by passive flexion of the elbow during the session. Interestingly, in a few minutes after the end of the session the responses of the cell to somatic stimulation decreased and than disappeared.

It is evident that whether neuronal discharges were related better to the Go cue or to the onset of the movement depended substantially on the response latency. This is summarized in Fig. 5, which shows for 100 cells, the distributions of coefficients of correlation (left) and of slopes (right) plotted against the neuronal response latencies. Figure 5A shows the distributions for the relationships “lead time/reaction time,” which characterizes the relation of the neuronal responses to the sensory cue. B shows the corresponding distributions for the relationships “response latencies/reaction time,” characterizing the relation to the onset of the movement. Observe in A that the relation of the discharges to the Go cue decreases with increasing response latencies. In contrast, B shows that the relation of the discharges to the onset of the movement increases with increasing response latencies. The latency histogram in C shows a clear separation of cells with latencies of 20–110 and that show cue-locked responses ($r$ and slope $>0.7$; cf. A) while cells with sensorimotor and motor responses overlap.

**Response patterns during reaching with the contra- versus the ipsilateral limb.** In the first part of the present study, the neurons in the motor cortex were divided into three types based on the responses
during reaching with the contralateral limb. The goal of the second part was to compare how the cells of the different types react when reaching is performed with the ipsilateral limb.

Three hundred sixty neurons were studied during reaching movements with the ipsi- and contralateral forelimb performed by cats NN 3–NN 6. Two hundred fifty-six of them with clear changes in activity during movements with the contralateral limb were selected for comparison of neuronal activity during performance with the different limbs. The group of discarded neurons consisted of 69 cells with weak excitatory or inhibitory responses irrespective of the forepaw used, 28 cells activated only after initiation of the reaching movement, and 7 neurons...
which changed activity selectively during reaching with the ipsilateral limb.

Responses to the sensory cue

The 256 cells were classified into four major groups according to their responses to the sensory cue when the reaching movement was made with the ipsi- versus the contralateral limb. The classification is summarized in Table 2.

CELLS WITH IDENTICAL SENSORY RESPONSES DURING IPSI- AND CONTRALATERAL MOVEMENTS. This group (1st column in Table 2) includes 29 cells that demonstrated sensory responses during movements with the ipsi- as well as with the contralateral limb. During reaching with the contralateral limb all cells had a biphasic response, in 25 cells it was biphasic-a and in 4 cells biphasic-b response pattern. A representative example is illustrated in Fig. 6. The experiment started with reaching performed by the ipsilateral limb. A clear short-latency (30 ms) sensory response to the Go stimulus is evident in the PSTH and in the raster plot. The raster plot also shows that the sensory response was followed by second, slightly stronger premovement activation that led the lift-off of the paw by 100 ms. During the same experimental session, the reaching movement was for the first time in this cat transferred to the contralateral limb. Figure 6, bottom, shows the activity of the same neuron during contralateral performance. It is evident that the Go stimulus generated a sensory response with the same parameters as during movements with the ipsilateral limb. The latency as well as the discharge frequency were similar. The cumulated number of spikes in all illustrated trials during the first 200 ms after the stimulus onset (i.e., spikes related to the cue), were 101 (4.33 ± 1.04) and 104 (4.13 ± 1.03), respectively and did not differ statistically (P = 0.43). The correlation of the lead times with the reaction times was also similar (0.92 and 0.96 for movements with the ipsi- and contralateral limb, respectively, P < 0.0001). The second component of the discharge
related to the movement was rather different when the different limbs were used. During reaching with contralateral limb, it developed 120 ms before the onset of the movement; this can be clearly seen as a change point of the discharge frequency in each individual trial (this is the same cell as in Fig. 4A). The highest discharge frequency was sustained at the same level for ~100 ms after the onset of the movement and was rather high throughout the entire movement. When the ipsilateral limb was used, the second component was also initiated ~120 ms before movement onset but with much less discharge frequency as compared with the that during contralateral reaching. After lift-off the frequency of these discharges decreased progressively and returned to background level within 200 ms.

In all 29 cells in this group, the discharge frequency and latencies of the sensory responses during ipsi- versus contralateral performance were similar, the latter ranged from 20 to 110 ms (64 ± 22). A second, movement-locked component was visually detectable in all cells during reaching with the ipsi-

---

TABLE 2. Classification and summary of response properties of all cells (n = 256) investigated

<table>
<thead>
<tr>
<th>Response During Movements With the Contralateral Limb</th>
<th>Response Pattern During Movement With the Ipsi-Versus the Contralateral Limb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Complex pattern with sensory response</td>
<td>Bilateral sensory responses</td>
</tr>
<tr>
<td>Biphasic-a</td>
<td>25</td>
</tr>
<tr>
<td>Biphasic-b</td>
<td>4</td>
</tr>
<tr>
<td>Sensorimotor response</td>
<td>—</td>
</tr>
<tr>
<td>Motor response</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
</tr>
</tbody>
</table>

The rows refer to the different response patterns during movements with the contralateral limb. The columns show the classification of the cells according to a comparison of their response patterns when the movement was performed with the ipsi- versus the contralateral limb.
neural limb, but it had much lower discharge frequency as compared with the contralateral reaching and progressively weakened right after the onset of the movement.

To verify that the sensory responses in the ipsilateral cortex were not solely due to the fact that the cats performed the task with either limb, a control experiment was made to show that such responses can also be observed in an animal trained with only one forepaw. In this animal, 5 of 15 cells recorded in the cortex ipsilateral to the limb performing reaching showed responses locked to the cue.

CELLS WITH SENSORY RESPONSES ONLY DURING IPSILATERAL MOVEMENTS. This group (2nd column in Table 2) included 31 neurons and is represented by the cell shown in Fig. 7. During reaching with the ipsilateral limb, the cell showed a sensory response with a latency of 60 ms (range: 40–120 ms for all cells in this group, mean: 71 ± 24). The onset of the discharge was clearly correlated to the onset of the sensory cue ($r = 0.86$, $P < 0.0001$). Note that there was no movement-related component after the sensory response, which made the firing pattern of this group of cells different from the cells discussed in the preceding text. During movements with the contralateral limb, the same cells instead showed a sensorimotor pattern correlated both with the onset of the sensory cue and with the onset of the movement. In the cell illustrated in Fig. 7, the response was initiated 240 ms after the sensory cue and had a significant correlation ($P < 0.001$) with both the Go cue and with onset of the movement. To summarize, the feature of these neurons is a pure (i.e., not followed by reduced movement-related activation) cue-locked response during reaching with the ipsilateral limb and a sensorimotor type of response during contralateral reaching.

FIG. 6. Example of effector independent sensory responses (during fast task). Activity is presented as PSTH and raster plots. The bin width in the PSTHs is 40 ms, and the number of cumulated trials ($n$) is 16. a, the onset of the sensory cue, short horizontal lines below histograms indicate the range of reaction times. The raster plots are ordered by increasing reaction time. The short vertical lines in the raster plots indicate the onset of the movement. The illustrated cell shows a biphonic response pattern during performance with the contralateral limb. During ipsilateral performance, the 1st component, i.e., the sensory response is similar, but the 2nd component, related to the movement, is reduced. The correlation coefficient ($r$) between the onset of the discharge and the onset of the stimulus is indicated above each raster plot as well as the regression coefficient (slope).

**CELLS WITH RECIPROCAL RESPONSE PATTERN DURING IPSI-VERSUS CONTRALATERAL MOVEMENTS.** This group (3rd column in Table 2) consists of 20 cells with reciprocal response pattern during ipsi- versus contralateral performance. A representative example is illustrated in Fig. 8 (the same cell as in Fig. 3B, but partially different selection of the trials). During reaching with the ipsilateral limb, the cell showed a short-latency inhibitory response locked to the onset of the Go signal (response latency = 40 ms, $r = 0.89$, $P < 0.0001$). Observe that both the onset and the offset of the inhibitory response were locked to the sensory cue and were not modulated by the onset of the
movement despite the fact that the response lasts >600 ms. The latency of the inhibitory responses ranged from 40 to 90 ms (62 ± 17) in different cells. During reaching with the contralateral limb, the cell showed a sensorimotor pattern. The response latency was 200 ms, and the correlation coefficients were 0.72 (P < 0.001) with the onset of the sensory cue and 0.85 (P < 0.0001) with the onset of the movement. Of 20 cells, 15 showed a sensorimotor response pattern during contralateral performance and the remaining 5 a biphasic-b response (cf. Table 2, column 3).

**CELLS WITH SIMILAR RESPONSES AND CELLS WITH VARIABLE RESPONSE PATTERNS.** This group (column 4 in Table 2) consists of 14 neurons with a sensorimotor response pattern and 11 cells with biphasic-b subtype of response pattern during reaching with the contralateral limb. Responses of the 14 cells with sensorimotor pattern were very similar regardless of the forepaw used. In contrast, among cells of the biphasic-b type rather high response variability from session to session was observed during reaching with the ipsilateral limb. Three such neurons (A–C) recorded during the slow task different daily sessions are illustrated in Fig. 9. All three cells were recorded at the same location of the electrode and are likely the same neuron. The day after recording from cell A, the electrode was moved to a new position. It was returned to the previous position (as for cell A) in two days and cell B was found. The recording from the cell C was made during the next day without any change of the position of the electrode. Therefore all three cells were registered at the same position. All of them had similar response patterns during movement with the contralateral limb (right). PTHs synchronized with the onset of the movement revealed a clear triphasic response pattern for all three neurons (cf. Fig. 4B2). During movements with the ipsilateral limb, each cell demonstrates a rather different response. The basic response pattern of the cell in A is a similar (i.e., multiphasic) during reaching with either limb. During reaching with the ipsilateral limb, the pattern is slightly reduced in amplitude and has the larger initial response, the latter is due to the fact that a simultaneously presented click and light were used as Go cue, whereas for the contralateral movement only a tone (cf. METHODS). The cell in B showed a marked reduction of the response when the movement was made with the ipsilateral limb as compared with the contralateral. The cell in C was tested during movements with the ipsilateral limb in the slow and the fast task in the same daily session. During the slow task, a short-latency excitatory response was present followed by short lasting suppression of activity (Fig. 9C1). Immediately

---

**FIG. 7.** Example of a cell with sensory responses during reaching performed by the ipsilateral limb (slow task). During the ipsilateral task, the responses of this cell have short latencies and are locked to the sensory cue. During the contralateral task, the cell shows a sensorimotor response. The activity has longer latency, and the time of onset is correlated with both the sensory cue and with the onset of the movement. Raster plots and PSTHs (n = 20) are displayed as in Fig. 1. The correlation coefficient (r) between the onset of the discharge and onset of the stimulus is indicated in the raster plots in A and B, above the time of presentation of the sensory cue (a). In the raster plot in B, the correlation coefficient between the onset of the discharge and the movement is indicated above the movement-related discharge.
after the slow task, the fast task was used, and the cell then responded to the same cue by deep and long-lasting suppression of activity (Fig. 9C2). To summarize, Fig. 9 illustrates that the cells of the biphasic-b type show a very variable response pattern from session to session during reaching with the ipsilateral limb. The somatosensory receptive fields of these cells were unstable and flexible. Sometimes the cells could be effectively activated by passive flexion of either forelimb, in a few minutes later, only contralateral or bilateral palpation of the whole forelimb was effective.

Neuronal responses in relation to the onset of the movement

The analysis in the preceding text shows that the sensory cue triggered pronounced stimulus-related activity in the motor cortex ipsilateral to the forelimb executing the reaching movement. Opposite to the contralateral motor cortex, the sensory responses in the ipsilateral cortex were not transformed into a motor command. This is illustrated in Fig. 10, which shows the activity of different types of neurons, synchronized at the onset of the movement, during ipsi- versus contralateral performance. It is evident that during contralateral performance, all neurons showed powerful activity related to the onset of the movement. In contrast, none of them was activated in relation to the onset of movements with the ipsilateral limb. Generally, most cells with a motor-related response during reaching with the contralateral limb did not respond at all when the ipsilateral limb was used (cf. Table 2, column 5).

Background activity during the ipsi- versus the contralateral task

In all cells, the mean background discharge frequency during the last 700 ms of the prestimulus period was compared when the reaching movement was performed with the ipsi-versus the contralateral limb (100 trials, 10-ms bin width). Thirty-one percent of the cells showed a statistically significant (P < 0.001) change of background activity when the performance was switched between limbs. Of all cells with task-dependent background discharge frequency, 54% had higher frequency when the cat was preparing for a movement with the contralateral limb, whereas 46% had a higher background activity during ipsilateral performance. Cells A, B, and D in Fig. 10 illustrate increased, and the cell in Fig. 6 decreased background activity during ipsilateral performance. For all such cells the ratio higher/lower background discharge frequency was between 150 and 200%.

FIG. 8. A neuron with reciprocal activity during ipsi- vs. contralateral performance (slow task). This cell has a sensorimotor response pattern during the contralateral task, like the cell in Fig. 2. During the ipsilateral task, the cell shows a short-latency inhibitory response locked to the onset of the cue. Note that the offset of the inhibitory response is also locked to the sensory cue. Raster histograms, PSTHs (n = 25), and statistical values displayed as in previous figures.
as reflecting the tuning of neuronal networks for effective control of the movement (cf. DISCUSSION). A certain pattern of background activity may be required for successful processing of the motor command. One possibility is that the change of background activity observed when the performance was switched between limbs reflects such tuning of the cortical networks and contributes to select the appropriate hemisphere for elaboration of the motor command. This supposition was tested in two cats trained to use different limbs for the reaching movement on presentation of two different cues. A light flash was used as a Go stimulus for the left limb, and a tone was used as signal for the right limb. When each signal was presented in separate blocks of trials, so that only the limb conditioned to the given Go cue was used, the performance level was usually 100%. When the two signals were presented randomly in the same session, so that the proper limb had to be selected on presentation of the cue, the level of performance dropped to 60% in one cat and to 68% in the second. A stable performance at a level of 93 and 85% in the two cats, respectively, was achieved after 13 and 18 days of training. The activity of 37 neurons was recorded in one cat during this test, and the background frequency was compared during ipsi- and contralateral performance as well as when both limbs were used intermixed. In 18 cells, the background frequency was modulated when the limb used for the movement was changed in separate blocks of trials. During the task with intermixed use of both limbs, the background frequency of these cells was either the same as in the task when the contralateral paw was used or was slightly shifted toward the value of the background discharge frequency observed during performance with ipsilateral limb. To exclude that the lower performance level during the test with intermixed reaching of both limbs was due to the use of two different Go signals in the same task, both cats were later retrained in a control experiment to perform a reaching task with one limb toward one of two pedals fixed on a frontal wall (interpedal distance: 7 cm). The same cues—light flash and tone—were used as signals to different pedals. In this task, a performance level near to 100% was achieved in a 3–5 days of training, suggesting that difficulties observed in the “intermixed test” are not caused by the increased complexity of the task in which two different Go signals are used.

**DISCUSSION**

The present results show that the elaboration of a motor command starts with a cue-locked activity well before the onset of reaching. This suggests encoding of high-order parameters of the movement by the motor cortex of the cat. Surprisingly, this cue-locked activity is equally well initiated in the motor cortex ipsilateral to the conditioned limb, but, in contrast to the contralateral cortex, is not followed by strong movement-related discharges. The cue-locked inhibitory responses in other cells of the ipsilateral cortex suggest that this reduction may be due to active suppression of the ipsilateral motor command. These findings indicate that ipsilateral cortical activity may be normally generated during unilateral motor tasks, although without serving any direct function for the initiation of reaching. Overall, the results contribute to the understanding of the ipsilateral cortical activation. It is also hypothesized that undesirable mirror movements in humans results from a deficient in active suppression of the ipsilateral activity.
Activity during movement with the contralateral limb

A first interesting finding of the present study is that some neurons in the motor cortex generate a biphasic response with short-latency cue-locked activity. The cue-locked response has previously been described in the forelimb area of the motor cortex of cat during isometric flexion-extension performed with very short (~100 ms) reaction time (Martin and Ghez 1985; Vicario et al. 1983). The principle difference of the present result is that sensory responses as short as 20 ms are observed during reaching movement performed with rather long reaction time (sometime >500 ms), indicating that relevant for the movement sensory cue can be detected by the motor cortex well before the onset of the motor response. This makes clear difference compared with the cortex of the monkey, in which the activity of the primary motor cortex may lead the onset of the motor response by >100 ms, but being nevertheless time-locked to the movement (Alexander and Crutcher 1990; Georgopoulos et al. 1984; Hocherman and Wise 1991; Humphrey and Tanji 1991; Kalaska et al. 1989; Thach 1978). However, a few studies, reported sensory responses in MI of the monkey (Lamarr et al. 1983, 1985; Riehle 1991; cf. also Houk et al. 1993). Another general finding on the monkey is that cue-locked activity can be observed in the premotor and supplementary motor areas (Kurata and Tanji 1985, 1986; Tanji 1985; Tanji and Kurata 1982, 1985). It seems therefore that cue-locked and movement-related activity in that monkey is separated between different motor cortical areas, is fused in the cat on the same motor cortical cell providing thus biphasic response pattern. Rather poor subdivision of the motor cortex in cat into primary and nonprimary areas supports this view (Ghosh 1997). Although the exact function of the short latency response is yet to be understood, they strongly indicate that the motor cortex of the cat is involved into early, hierarchically higher stages of the sensory to motor transformation.

Activity during ipsilateral movement

A salient finding of the present study is that cue-locked discharges are equally well represented in the motor cortices of both hemispheres despite the fact that movement-related activity is further developed only in the cortex contralateral to the acting limb. Therefore the neurons in the motor cortex ipsilateral to the moving limb may respond to the Go stimulus. All cells with biphasic discharge pattern respond similarly to the Go cue whatever limb is used, but the movement-related component of the discharge develops properly only in the
contralateral motor cortex. The observation of sensory responses in the ipsilateral cortex was quite unexpected because, as it was shown in case of the contralateral motor cortex, a strong sensory response is invariably followed by a late movement-related discharge in the same cell and is always associated with execution of a reaching. Accordingly, the sensory responses in the ipsilateral motor cortex may indicate that during preparation for a unilateral movement identical mirror commands for the opposite limb is initiated. There may be at least two possible explanations of the ipsilateral activity. First, it has previously been suggested that the motor cortical areas may encode abstract features of the movement (Cisek et al. 2003; Perfiliev 1998; Rijntjes et al. 1999). In this way, such effector-independent activity may serve as basis for “motor equivalence,” i.e., the ability to execute a movement learned with one extremity by another limb (Lashley 1930). Second, a certain degree of ipsilateral activity can be due to a high potential of any interconnected cortical areas for undesirable coactivation (see for review Clark 1996; Houghton and Tipper 1996), which is prevented normally by inhibitory connections between adjacent points (Schneider et al. 2002). Potent callosal connections between the motor cortical areas have been demonstrated (cf. Gould et al. 1986; Innocenti 1986; Marconi et al. 2003; Matsunami and Hamada 1984; Rouiller et al. 1994; Schnitzler et al. 1996).

**Rivalry between two cortices**

Bilateral triggering of sensory responses initiates elaboration of two conflicting commands, which in turn, may generate a competition between the two motor cortices. As will be discussed later, one of the key factors preventing further development of the motor command in the ipsilateral cortex may be specific background activity of the ipsilateral cortical network. Several findings suggest nevertheless that to prevent further elaboration of the “mirror” command and to avoid initiation of a movement with the wrong limb, a cortical inhibitory command is required. Two competing trends—one to elaborate a mirror command in the ipsilateral cortex and another to abort it—were observed during unilateral movements in humans (Kobayashi et al. 2003; Zaaroor et al. 2001). An active inhibitory command to the side not to be moved during preparation for a unilateral thumb movement was also suggested by Leocani et al. (2000) and Liepert et al. (2001). As a component of such an inhibitory command one can consider the group of neurons observed in the present study showing reciprocal response pattern with short-latency suppression of the activity when the ipsilateral limb was used (Fig. 8). It is not clear whether the stimulus-locked inhibitory responses of these neurons are triggered in the ipsilateral cortex directly due to its special background activity or if they are induced via the contralateral hemisphere. The latter possibility is suggested by a number of recent data showing that transcranial magnetic stimulation of the motor cortex in one hemisphere can inhibit voluntary movements or electromyographic responses initiated by contralateral side (Ferbert et al. 1992; Kujirai et al. 1993; Lazzaro et al. 1999; Meyer and Voss 2000; Meyer et al. 1995). This inhibition is markedly reduced after agenesis or lesions of the corpus callosum (Meyer et al. 1995; Rothwell et al. 1991).

It was also found in this study that some cells exhibited a fully developed sensorimotor or biphasic-b response during movements with the ipsilateral limb (cf. Fig. 9A). This may indicate that complete abortion of the developing mirror command is difficult, and it is developing to some extent despite active suppression.

It is also noteworthy that the reciprocal responses observed during ipsi- and contralateral movements are quite similar to those described during a flexion-extension task (Crutcher and Alexander 1990; Evarts 1974). This may suggest that a similar rivalry takes place between cortical representations of the antagonistic muscles of the same limb. The possibility of a command for suppression of the antagonistic muscle is suggested by the finding of a suppression of the antagonists before activation of the agonists in fast voluntary flexion movements (Hallett et al. 1975).

Overall, together with the data cited in the preceding text, the present findings suggest that selection of high-order cortical commands may be achieved via mechanisms similar to the reciprocal control of muscle activation at the level of the spinal cord.

**Origin of the ipsilateral activity**

It is highly unlikely that the observed ipsilateral cortical activity can be related to postural control. First, EMG recording revealed that in most of the trials performed during the fast task, the EMG activity of the supporting limb did not lead the onset of reaching, suggesting that the postural adjustments required for the initiation of the reaching were made in those trials before presentation of the Go cue. Moreover, the longest lead time of the EMG activity in the trials performed with reaction times exceeding 700 ms was no more than 200 ms. In the very same trials, cue-locked activity with a latency of 20–100 ms could be observed. Such early discharges could therefore not be related to EMG activity. All electrode penetrations were located in the forelimb areas, and the somatic receptive fields of all cells were within the forelimb indicating that their activity was not related to the control of axial muscles.

Next important issue is whether the ipsilateral sensory responses are due to rapid transfer of the contralateral cortical activity or rather were established during learning and are afterward triggered independently and simultaneously in both cortices? Both possibilities could be admitted considering that rather dynamic interhemispheric interaction can be observed as during initial training (Gerloff and Anders 2002; Kogan et al. 1978; Sperry 1968) as in case of preparation for the execution of the well-established task (Kobayashi et al. 2003; Leocani et al. 2000; Liepert et al. 2001; Zaaroor et al. 2001). Nevertheless the rather low conduction velocity of the callosal fibers makes the possibility of rapid and precise exchange between hemispheres questionable (Ringo et al. 1994). Moreover, the same latency value of the sensory response during performance with the ipsi- versus contralateral limb speaks for the independent initiations of the ipsilateral activity. Similarly, in the same paradigm, we observed no latency difference of the earlier component of the evoked potential recorded simultaneously from both motor cortices (Nikulin et al. 1996). Altogether, it seems reasonable to suggest that the basic pattern of neuronal responses to the Go cue in the ipsilateral cortex is established during initial training.
Some cells in the present study showed cue-locked responses during ipsilateral movement only. One may speculate that in the ipsilateral neuronal network, which is not tuned for movement execution, the sensory responses were unmasked in those cells, giving this hemisphere an advantage in detecting a relevant signal.

**Background activity**

An additional factor, which may facilitate elaboration of the motor command in the proper cortex and suppress its development in the ipsilateral hemisphere may be the rate of neuronal background discharge. It is well known that during motor tasks proper tuning of background discharge frequency, i.e., set related activity, is important for effective performance (Favorov et al. 1988). In the cat, it has been shown that many motor cortical cells change their background discharge frequency during task performance compared with the firing level during rest (Cherenkova et al. 1987).

In the present experiments, 31% of the cells showed statistically significant changes in background activity when the performance was switched between the two limbs in different blocks of trials. Such limb-specific differences in background activity was not found when both limbs were used intermixed and with different Go-stimuli for each limb. Instead, most of the cells tended to show a level of background activity typical for the tasks in which only the contralateral limb was used. This suggests that in this paradigm both cortices should have a similar background activity and that both are tuned for motor performance. Accordingly, in this task, differences in background activity cannot contribute to selection of the limb. As it was expected, under such conditions the accuracy of the stimulus-limb selection was decreased, i.e., given Go cue initiated more often a movement of the wrong limb. This result is consistent with the idea that certain pattern of background activity facilitates the selection of the limb to be initiated in response to the sensory cue. Drastic change of the background activity was also observed in a primary motor cortex of the monkey when the performance was switch between arms (Cisek et al. 2003).

To summarize, the present results show that the programming of a unilateral movement is not limited to elaboration of the command in the contralateral motor cortex but also includes generation of a mirror command in the ipsilateral motor cortex that needs to be actively inhibited. It is also suggested that deficits in the inhibition of the mirror command result in undesirable mirror movements.

**Acknowledgements**

The experimental data were obtained in the Laboratory of Sensorimotor Systems, St. Petersburg State University and analyzed at Dept. of Physiology, Göteborg University. The author is indebted to Prof. G.A. Kulikov, Prof. A. Lundberg, and Dr. L.-G. Pettersson for discussions and comments on the manuscript.

**Grants**

This work was supported by Russian state grants, the Swedish Medical Research Council (project number 11589), and Knut och Alice Wallenbergs Stiftelse.

**References**


REACHING AND THE IPSI-/CONTRALATERAL MOTOR CORTICES


