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Neuronal Correlates of Sensorimotor Association in Stimulus–Response Compatibility

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Neuronal mechanisms underlying stimulus–response (S-R) associations in S-R compatibility tasks were identified in 2 experiments with monkeys. Visual stimuli were presented on the left and right calling for left–right movements under congruent and incongruent S-R mapping instructions. High- and low-pitched tones calling for left–right movements were presented to the left and right ear, and the stimulus side was irrelevant. Single neurons sensitive to the S-R mapping rule were found in the primary motor cortex. The large overlap between the neuronal populations sensitive to the stimulus side, the S-R mapping rule, and the response side, respectively, is consistent with the idea that sensory-to-motor transformation is a continuous rather than a discrete process. Results partly support the hypothesis that the increase in reaction time with incongruent mapping is caused by the automatic activation of the congruent, but erroneous, response.

The study of neuronal mechanisms underlying the association of sensory inputs and motor outputs is key to understanding the nature and acquisition of skills. A behavioral paradigm that seems ideally suited to address this issue is *stimulus–response compatibility* (SRC), so named by Paul Fitts, who first reported it (Fitts & Deininger, 1954; Fitts & Seeger, 1953). Here, stimuli and responses are paired in different ways to construct tasks in which performance (i.e., reaction time [RT] and accuracy) is determined not by stimulus or response factors alone but by their interactions (i.e., their association). For example, if the stimuli consist of two lights, one on the left and the other on the right, and the responses consist of two keys, one on the left and the other on the right, performance is better if the responses are made with ipsilateral keys than with contralateral keys. This is true regardless of whether the responding limbs themselves are ipsilateral or contralateral, thus eliminating anatomical factors as the basic cause. SRC effects are among the most robust findings in the behavioral experimental literature (for recent reviews, see Kornblum, 1992; Proctor & Reeve, 1990), and reflect central cognitive associative processes.

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Kornblum, Hasbroucq, and Osman (1990) proposed a general model of SRC effects. According to the model, the dimensional overlap (DO) model, if the dimensions or attributes of a stimulus set are perceptually, structurally, or conceptually similar to those of the response set (i.e., if the dimensions overlap), then the presentation of a stimulus element automatically activates its corresponding response element. If the mapping instructions define this automatically activated response as correct (congruent mapping), then it is executed quickly; if the mapping instructions define a different response as correct (incongruent mapping), then the automatically activated response is first aborted, the correct response is identified, and it is then executed. Both the abort and the response identification process in the latter cases add to the time required for the execution of the correct response.

Automatic activation of a response is not restricted to the case in which the overlap is between the relevant stimulus dimension and the response. It also occurs if the irrelevant stimulus dimension overlaps with the response. One of the earliest such examples is from a study by Simon and Small (1969), who instructed subjects to press a left key to a high-pitched tone and a right key to a low-pitched tone. The tones were randomly presented to the left and the right ear. Although the stimulated ear was irrelevant to the performance of the task (i.e., its correlation with the response was zero and subjects were instructed to ignore it), RT was faster when the side of the response key and the side of the stimulated ear corresponded than when they did not correspond.

Although SRC effects tap into the nature of the linkages between sensory input and motor output, few attempts have been made to study the neural basis of these effects. Some evidence supporting the DO model's automatic response activation hypothesis has been obtained from psychophysi-

ological studies (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; Osman, Bashore, Coles, Donchin, & Meyer, 1992). Subjects in those experiments performed a two-choice RT task in which visually displayed letters were mapped onto a left or right keypress response. The stimulus letters were flanked by other letters that were either compatible or incompatible with the response. By recording the lateralized readiness potential (i.e., a change in the evoked brain potential that develops over the motor cortex contralateral to the overt response), it was found that in trials in which the stimulus was flanked by incompatible noise, both responses were initially activated, with the incompatible response eventually dropping out and the compatible one being left to be executed, with a delay.

As far as we know, few studies have addressed the question of sensorimotor association at the single-neuron level. Neurons have been found in monkey premotor (PM) and prefrontal (PF) cortices whose changes in activity differed depending on the degree to which the response signal (RS) and target were spatially contiguous during a pointing task (Di Pellegrino & Wise, 1993). With a similar task, Crammond and Kalaska (1994) presented a visual precue either on the same (congruent) or on the opposite (incongruent) side of a subsequent movement and found PM neurons that showed two successive activations during the delay between the precue and the RS. The first activation was related to the location of the precue and the second to the direction of the movement. In another study (Vaadia, Gottlieb, & Abeles, 1982), single-neuron activity was recorded in a monkey who was performing a task in which the mapping between the two stimuli (a tone or a noise) and the two responses (either a right or a left level shift) was changed from one block of trials to the next. The activity of 9% of the neurons recorded in the auditory cortex was found to differ not only according to the stimulus type but also the stimulus–response (S-R) mapping rule. Vaadia et al.'s study is more closely related to reversal learning than to SRC. Because there was no DO between the set of stimuli and the set of responses, neither mapping could be called congruent or incongruent (see Kornblum et al., 1990). Consequently, RTs—which were unfortunately not reported—were not expected to differ between mappings.

However, there are two single-neuron studies in the literature whose results are easily interpreted as SRC effects. First, Georgopoulos, Lurito, Petrides, Schwartz, and Massey (1989) and Lurito, Georgakopoulos, and Georgopoulos (1991) trained a monkey to move a handle either toward (congruent trials) or in a direction perpendicular to (incongruent trials) a stimulus light and found that the RT was longer in the incongruent than in the congruent condition. The weighted sum of the contributions of the directionally tuned neurons—what Georgopoulos et al. (1989) called the "neuronal population vector"—in the motor cortex pointed in the direction of the stimulus (i.e., the congruent movement) at the start of incongruent trials before rotating in the direction of the required, incongruent movement. Although those authors interpreted these data within the framework of the mental rotation paradigm, the results are perfectly consistent with the automatic response activation hypothesis that, in incongruent trials, the congruent, inappropriate movement is automatically activated, then aborted, before the correct, incongruent movement is initiated. In a second study, Alexander and Crutcher (1990) trained 4 monkeys to move a cursor to track targets on a display screen by extending or flexing the forearm. The cursor and forearm moved either in the same (congruent) or in the opposite (incongruent) direction in separate blocks of trials. Changes in neuronal activity, time locked to either target displacement or forearm movement, were found in the primary motor (MI) and PM cortices during the foreperiod and movement execution. Although Alexander and Crutcher mentioned that a significant proportion of neurons had movement-related activity that depended on the direction of the target displacement rather than the direction of the movement, they unfortunately did not test for the interaction of these factors.

In two experiments, we addressed the issue of identifying the neuronal mechanisms underlying SRC effects by recording changes in single-neuron activity in MI of monkeys while they were performing spatial SRC tasks. In Experiment 1, SRC was manipulated by changing the mapping of the relevant stimulus dimensions onto the responses (Type 2 ensembles in Kornblum's taxonomy; Kornblum, 1992; Kornblum et al., 1990). In Experiment 2, SRC was manipulated by changing the consistency of the irrelevant stimulus dimensions and the responses (Type 3 ensembles in the Kornblum taxonomy). In both experiments, we were especially interested in identifying a possible neuronal code for the S-R association rules that defined congruent and incongruent and consistent and inconsistent S-R relationships, as well as the neuronal correlates of the automatic activation of the congruent and consistent, but incorrect, response in the incongruent mapping. These two objectives justified focusing the recordings on MI. First, it was previously shown (Requin, Riehle, & Seal, 1988, 1992; Riehle & Requin, 1989; Miller, Riehle, & Requin, 1992) that MI neurons may be classified according to the timing properties of their activity. "Sensorimotor" neurons in particular display two successive activity components, one stimulus related and the other movement related. These neurons therefore seemed to be good candidates for coding the S-R association rules. Second, automatic activation of the congruent incorrect response during the incongruent mapping condition would be expected to produce changes in the activity of the MI neurons that control this response. Preliminary results of Experiment 1 have been presented elsewhere (Riehle, Kornblum, & Requin, 1994).

Experiment 1

In this first experiment, SRC effects were manipulated by mapping the left–right spatial location of a visual stimulus onto the left–right pointing movements that were used as the response congruently and incongruently.

Method

Materials and experimental design. Two male monkeys (1 *Macaca fascicularis* [6 kg] and 1 *Macaca mulatta* [10 kg]) served

as subjects. Subjects were cared for according to the Guiding Principles in the Care and Use of Animals of the American Physiological Society. Subjects held a pointer by a vertical handle and were trained to move the pointer in the horizontal plane by flexion and extension movements of the wrist. The axis of rotation of the pointer was under the wrist. The pointer was enclosed by a concave, semicircular vertical panel and terminated 5 mm from the panel. Three vertical pairs of light emitting diodes (LED) were mounted on the panel, one pair in the middle and one pair each 40° to the left and right of the central pair. The central pair consisted of two white LEDs, 1 cm apart, that were continuously on and marked the starting position of the movement. The other two pairs consisted of a yellow LED 1 cm above a blue one. These two side pairs served as the RSs and movement targets when they were on (cf. Figure 1).

To start a trial, the monkey had to align the pointer with the starting position and hold it there. After a 2-s delay, one of the four colored side LEDs went on. For one monkey, if the LED was yellow he had to align the pointer with this LED (congruent mapping), and if the LED was blue he had to align the pointer with the LEDs on the opposite side (incongruent mapping). For the other monkey, this mapping was reversed. To obtain pointing movements that were as rapid and as accurate as possible, monkeys were rewarded with a drop of apple juice only when movements were both fast and accurate. The criterion time consisted of the RT (i.e., the time between the target onset and movement start) and the movement time (MT; i.e., the time between movement start and movement termination). These temporal windows were gradually reduced during training.

Congruent and incongruent trials were blocked during the training sessions and alternated from one session to the next. After the monkeys had learned the two mappings (i.e., when a criterion of more than 80% correct was met in both conditions), they underwent the surgery required to record single-neuron activity. After surgery, the congruent and incongruent trials were randomly intermixed within each daily session, and single-neuron recordings started on the first day of such intermixed sessions. Each recording session included at least 20 trials of each of the four types of trials formed by combining the two types of movement (extension and flexion) with the two mapping conditions (congruent and incongruent). Only recording sessions were analyzed in which the animal performed the task correctly using the 80% criterion for each type of trial.

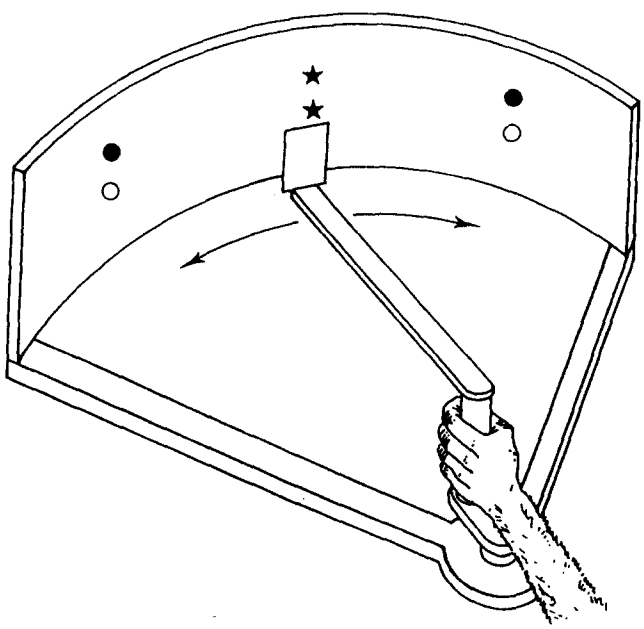

Figure 1. Experimental apparatus showing the pointer and the display panel with the light emitting diodes (LED) that indicate the starting position for movements (stars) and the target stimuli for congruent (black circles) and incongruent (white circles) mapping conditions in Experiment 1.

Surgical and recording techniques. Surgery was performed under halothane anesthesia (<0.5% in air). After an initial training period of about 4 months, a rectangular Perspex chamber (inner dimension = 10 × 26 mm) was placed over the contralateral MI (the right hemisphere for both monkeys). A mechanical device made it possible to fix the chamber and thus the animal's head during recordings. Glass-insulated tungsten microelectrodes (impedance = 0.5–1.5 MΩ at 1000 Hz) were inserted transdurally within the cortex by controlling the vertical displacement with a hydraulic micromanipulator. The *x–y* position of the electrode was referred to a 20 × 16 coordinate system in 0.5-mm steps, which was then superimposed over the cortical surface after the animal was killed with an overdose of pentobarbital for histological control (see Riehle & Requin, 1989, for further details).

Data analysis. A 486 microcomputer was used to control the LEDs and to store the behavioral and neuronal data. These data consisted of the RT, MT, action potentials, and the mechanogram of the movement. The mechanogram was generated by a linear potentiometer coupled with the axis of the handle that was sampled at 500 Hz. The time between the occurrence of the RS and a 0.5° deflection of the output of the potentiometer was defined as the RT, and the time between the RT and the pointer stopping within 0.5° of the final target position was defined as the MT.

Raster displays of neuronal activity and mechanograms were available on-line on the computer screen. Neuronal activity was pooled for each of the four types of trials and displayed in the form of rasters, with trials being rank-ordered according to RT, and in form of either peristimulus time histograms (i.e., time locked to the occurrence of the RS) or periresponse time histograms (i.e., time locked to movement onset) using a 40-ms bin width.

Results

Behavioral data. Monkey 1 participated in 27 recording sessions and Monkey 2 in 33 recording sessions. RTs and MTs were submitted to a two-factor (Stimulus Side × Response Side) analysis of variance (ANOVA) with repeated measures.

In Monkey 1 (cf. Figure 2), RT was significantly shorter for a right (328 ms) than for a left (382 ms) stimulus, $F(1, 26) = 57.66$, $p < .001$, and for a left (extension movement; 347 ms) than for a right (flexion movement; 368 ms) response, $F(1, 26) = 4.99$, $p < .05$. The interaction between these two factors, Stimulus Side × Response Side, was significant, $F(1, 26) = 27.94$, $p < .001$, thus demonstrating an SRC effect. RT was also shorter in the congruent (336 ms) than in the incongruent (374 ms) mapping condition. Highly similar differences also were found in MT: MT was shorter for a right stimulus (234 ms) than for a left stimulus (238 ms), but not significantly so, $F(1, 26) = 2.42$; however, MT was significantly shorter for a left (208 ms) than for a right (264 ms) response, $F(1, 26) = 375.52$, $p < .001$. The difference in MT between congruent (227 ms) and incongru-

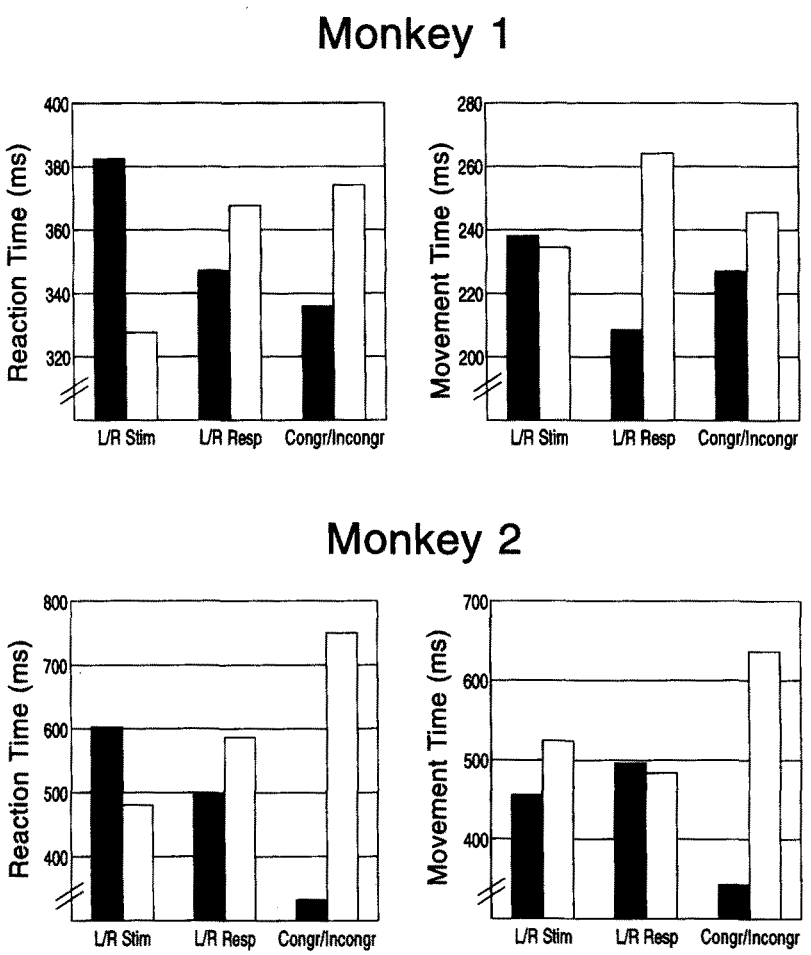

Figure 2. Reaction time and movement time for Monkeys 1 and 2 as a function of stimulus (stim) side (left [L] = black columns; right [R] = white columns), response (resp) side (left = black columns; right = white columns), and stimulus–response compatibility conditions (congruent [congr] = black columns; incongruent [incongr] = white columns) in Experiment 1.

ent (246 ms) trials also was highly significant, $F(1, 26) = 94.63, p < .001$.

A similar pattern was found in the RT data for Monkey 2. RT was significantly shorter for a right (480 ms) than for a left (602 ms) stimulus, $F(1, 32) = 193.61, p < .001$, and for a left (extension movement; 496 ms) than for a right (flexion movement; 586 ms) response, $F(1, 32) = 57.43, p < .001$. The interaction between these two factors was highly significant, $F(1, 32) = 267.02, p < .001$: RT for the congruent mapping condition (333 ms) was shorter than for the incongruent mapping condition (750 ms). The MT data had a different pattern than did the RT data. Movement times were significantly shorter for a left (455 ms) than for a right (524 ms) stimulus, $F(1, 32) = 44.77, p < .001$, and did not differ significantly between left (496 ms) and right (483 ms) responses. However, the interaction between these factors was highly significant, $F(1, 32) = 670.14, p < .001$, with MT for congruent mapping being shorter (343 ms) than for incongruent mapping (637 ms).

Physiological data. Changes in the neuronal activity of 277 neurons in MI (154 in Monkey 1 and 123 in Monkey 2; cf. Figure 3) were analyzed in three ways: The first analysis focused on the sensitivity of these changes to stimulus and response sides during the RT and MT periods. The second analysis focused on the timing of these changes with respect to stimulus onset and movement start. The third analysis focused on the neuronal correlates of the automatic response activation hypothesis (i.e., activation of the congruent but incorrect response in incompatible trials; Kornblum et al., 1990).

Sensitivity of changes in neuronal activity to external events. For each neuron, an ANOVA with repeated measures was conducted on the mean frequency of neuronal activity during the RT period (i.e., between stimulus onset and movement start), with stimulus side and response side as factors. Stimulus side had a statistically significant effect ($p < .05$) in 134 neurons (48%), and response side had a statistically significant effect ($p < .05$) in 157 neurons (57%). The Stimulus Side × Response Side interaction (i.e., the SRC effect) was statistically significant ($p < .05$) in 114 neurons (41%). Sixty-three neurons (23%) were not sensitive to stimulus side, or to response side, or to their interac-

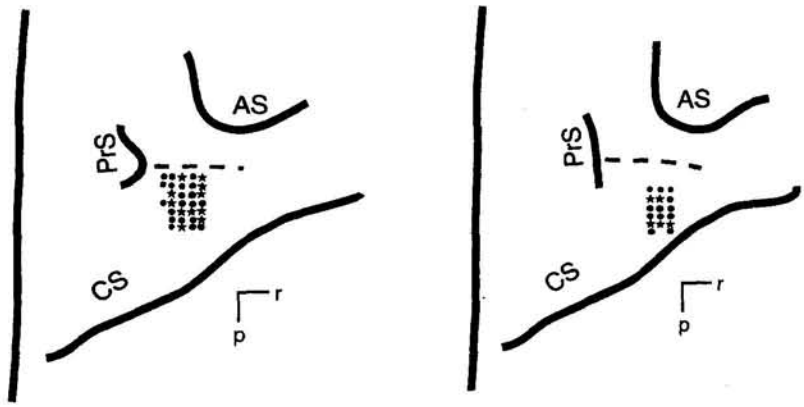

Figure 3. Anatomical location of electrode penetrations in Experiment 1. Stars indicate the sites where neurons were found whose changes in activity were sensitive only to stimulus–response compatibility effects. Data for Monkey 1 are on the right and those for Monkey 2 on the left. The dashed line corresponds to the borderline between the primary motor and premotor cortices. r = right, p = posterior; CS = central sulcus; AS = arcuate sulcus; PrS = precentral sulcus.

tion (see also Table 1). Note that the sum of the percentages of neurons with significant main effects or interactions exceeded 100% because a number of neurons were involved in two or more effects. These various neuronal populations are shown in Figure 4A. Examples of neurons whose changes in activity during RT were sensitive to stimulus side, response side, or the interaction of these two factors, are shown in Figures 5, 6, and 7, respectively.

Of special interest were the 18 neurons for which the only statistically significant effect was the Stimulus × Response Side interaction (as illustrated in the neuron in Figure 7). These neurons may be considered as exclusively coding the S-R association rule. Among these 18 neurons, 14 showed a larger activation with congruent than with incongruent S-R mapping, whereas 4 neurons showed the reverse.

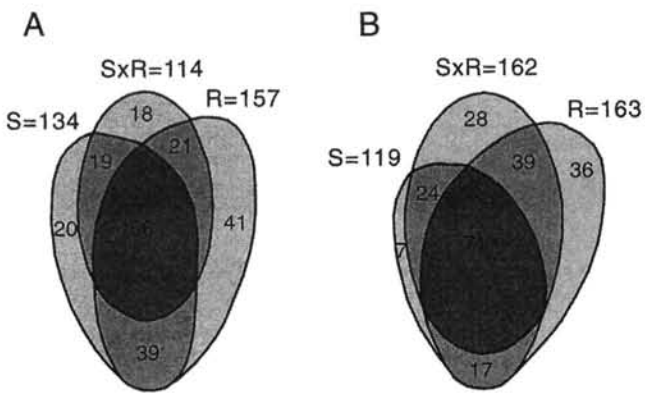

Figure 4. The three classes of neurons whose changes in activity during the reaction time period (A) and the movement time period (B) showed significant effects (on the basis of analysis of variance results) of stimulus side (S), response side (R), or Stimulus × Response Side interaction (S × R) in Experiment 1. Each of these neuron types is represented by a separate area. Where these areas intersect, we have represented the size of their overlapping and nonoverlapping sections as being proportional to the number of neurons (indicated within these areas) found in the various subclasses of neurons.

Because SRC was found to affect MT and RT, a similar repeated measures ANOVA was conducted on the mean frequency of neuronal activity during the MT interval. Stimulus side had a statistically significant effect ($p < .05$) in 119 neurons (43%), and response side had a statistically significant effect ($p < .05$) in 163 neurons (59%). The Stimulus Side × Response Side interaction was statistically significant ($p < .05$) in 162 neurons (58%), more than were found in the RT period. Furthermore, of these, 28 were sensitive only to the interaction, again, more than in the RT period ($n = 18$; see also Table 1). Fifty-five neurons were not sensitive either to stimulus side, response side, or to the interaction of these two factors. Once again, the sum of these percentages exceeded 100% because a number of neurons were involved in two or more of these effects. These various populations of neurons are shown in Figure 4B.

A comparison of the various areas in the topographical representations of Figures 4A and 4B reveals how the number of neurons whose change in activity depended on stimulus side, response side, or their interaction changed between the RT and the MT periods. The numbers of neurons whose discharge frequency was sensitive either to stimulus side only or to both stimulus side and response side decreased significantly between the RT (20 and 39, respectively) and the MT period (7 and 17, respectively), χ^2s (3, $N = 253$) = 8.66 and 9.10, ps $< .05$ and .01, respectively. The numbers of neurons whose discharge frequency was sensitive either to the Stimulus × Response Side interaction or to this interaction and response side increased significantly from the RT (18 and 21, respectively) to the MT period (28 and 39, respectively), χ^2s (3, $N = 278$) = 12.18 and 6.05, ps $< .001$ and .02, respectively.

Table 1 shows the tracking of neurons as their sensitivity changed from the RT to the MT period. About one fourth of

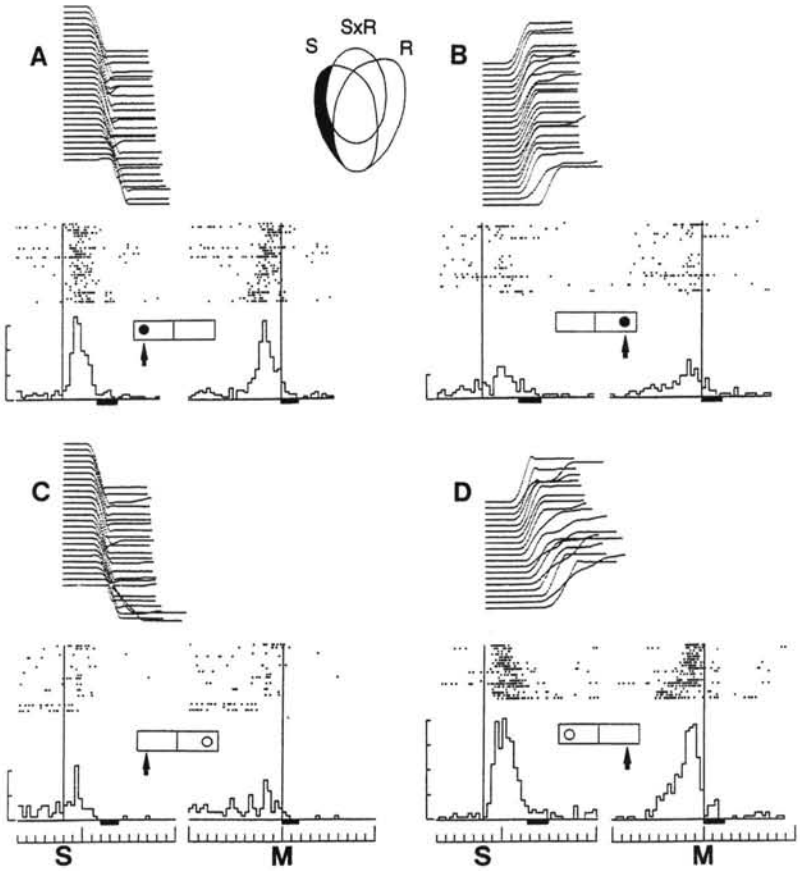

Figure 5. Example of a neuron that, on the basis of the analysis of variance, was significantly more activated during the reaction time period when the stimulus was presented on the left side (A and D) than on the right (B and C) in Experiment 1. The subclass of neurons in which this neuron was included is indicated by a black area within the insert that represents the Venn diagram in Figure 4A. Stimulus side was the only statistically significant effect for this neuron. Neuronal activity was pooled separately for each of the four types of trials (two stimulus sides × two response sides); the stimulus side is indicated by a circle and the response side by an arrow. The circle and arrow are on the same side for congruent trials (A and B) and on opposite sides for incongruent trials (C and D). Neuronal activity is displayed in the form of raster displays in which each line corresponds to one trial and each dot to one action potential. The trials are rank-ordered from top to bottom according to increasing reaction time. Neuronal activity also is displayed as frequency histograms using a 40-ms bin width. Both raster displays and frequency histograms are time locked either to stimulus presentation (S) or to movement onset (M). Changes in the potentiometer output, rank-ordered in the same manner as the raster displays, are shown at the top of each panel. Mean movement durations are indicated by horizontal black bars. Horizontal tick marks = 100 ms; vertical tick marks = 10 impulses/s. At top, S = stimulus side; S × R = Stimulus × Response Side interaction; R = response side.

all the analyzed neurons (71 of 277; 25.6%) did not change their response characteristics, (see Table 1). However, many more neurons either changed their functional property (e.g., a neuron that was sensitive to stimulus side during RT became sensitive to movement side during MT); acquired a new functional property between the RT and the MT period (e.g., a neuron that was sensitive to stimulus side during RT became sensitive to both stimulus side and response side during MT); or lost a functional property (e.g., a neuron that was sensitive to both the stimulus side and the response side during RT became sensitive only to the response side). These data confirm the hypothesis of a functional sensory-to-motor shift in neuronal activation from the RT period to the MT period by showing that, in general, the number of neurons that were more sensitive to stimulus side during the RT became more sensitive to either response side or SRC during the MT (cf. Figure 8). In Figure 8, only neurons have been taken into account whose change in activity, during both RT and MT, was clearly classifiable in the context of a functional sensory-to-motor shift. In other words, neurons

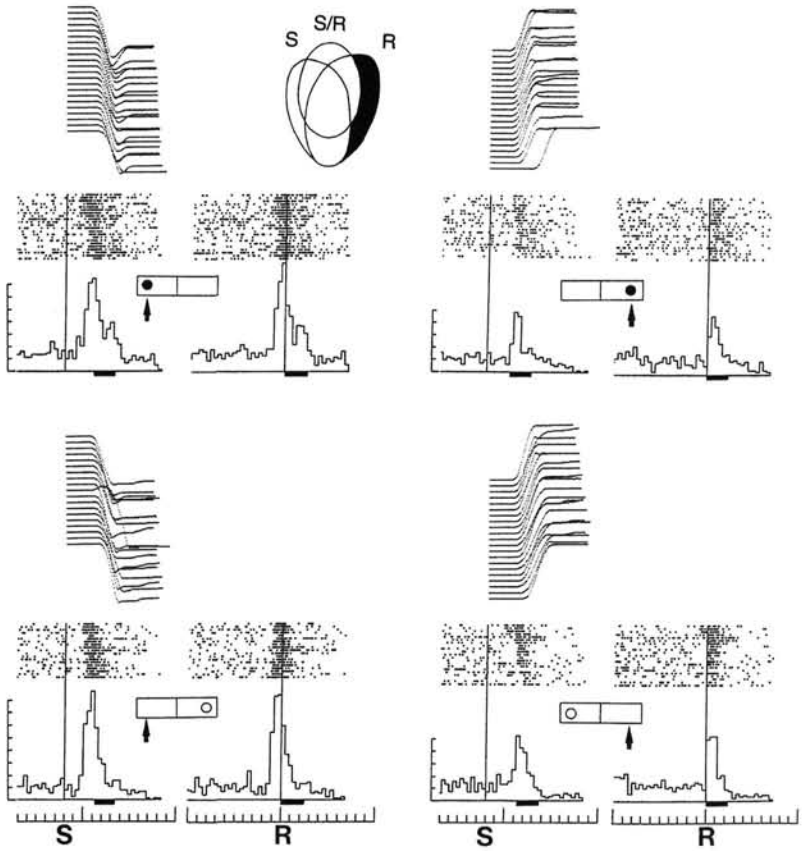

Figure 6. Example of a neuron for which activation during the reaction time period was significantly higher for leftward movements (A and C) than for rightward movements (B and D) in Experiment 1. Response side was the only statistically significant effect shown by the analysis of variance. The presentation was the same as in Figure 5. S = stimulus presentation; At top, S = stimulus side; S/R = Stimulus × Response Side interaction; R = response side.

whose change in activity was sensitive to both stimulus side and response side were discarded from the analysis.

Timing of changes in neuronal activity. The second way to analyze task-related changes in neuronal activity is to examine the timing of these changes with respect to external or behavioral events (i.e., stimulus onset and movement start). Recall that the raster displays of neuronal activity were rank-ordered according to RT. By aligning the neuronal activity to either stimulus onset or to movement start, it was relatively easy to determine by visual inspection whether the changes in neuronal activity were time locked to the one, the other, or both. Of the 277 neurons that were examined, unequivocal stimulus-locked changes in activity were found for 17 neurons, movement-locked changes for 156 neurons, and changes time locked to both for 67 neurons. The latter neurons either showed two successive changes in activity, with the first stimulus locked and the second movement locked, or they showed changes in activity that started with stimulus onset and ended with movement start. Examples of these three classes of neurons are shown in Figure 9. Thirty-seven neurons could not be classified.

Relationship between two measures of sensitivity: ANOVA and timing. Now that we had two different procedures for classifying neurons on the sensorimotor continuum, we assessed the degree to which the results of these two classification schemes converged. To simplify this comparison, we collapsed the seven categories of neurons that resulted from the ANOVA (cf. Figure 4A) into three categories: (a) neurons were included that were more likely to be involved in sensory than in motor processing. This included neurons that were sensitive only to stimulus side ($n = 20$) and neurons that were sensitive to both stimulus side and the Stimulus Side × Response Side interaction ($n = 19$). We called these "sensory-related" neurons ($n = 39$). (b) Neurons were included that were more likely to be involved in motor than in sensory processing. This included neurons that were sensitive only to response side ($n = 41$) and neurons that were sensitive to both response side and the Stimulus Side × Response Side interaction ($n = 21$). We called these "motor-related" neurons ($n = 62$). (c) Neurons were included that were more likely to be involved in the association between sensory inputs and motor outputs. This included neurons that were sensitive to both stimulus side and response side ($n = 39$), to the Stimulus × Response Side interaction ($n = 18$), and to both main factors and their interaction ($n = 56$). We called these "sensorimotor-related" neurons ($n = 113$).

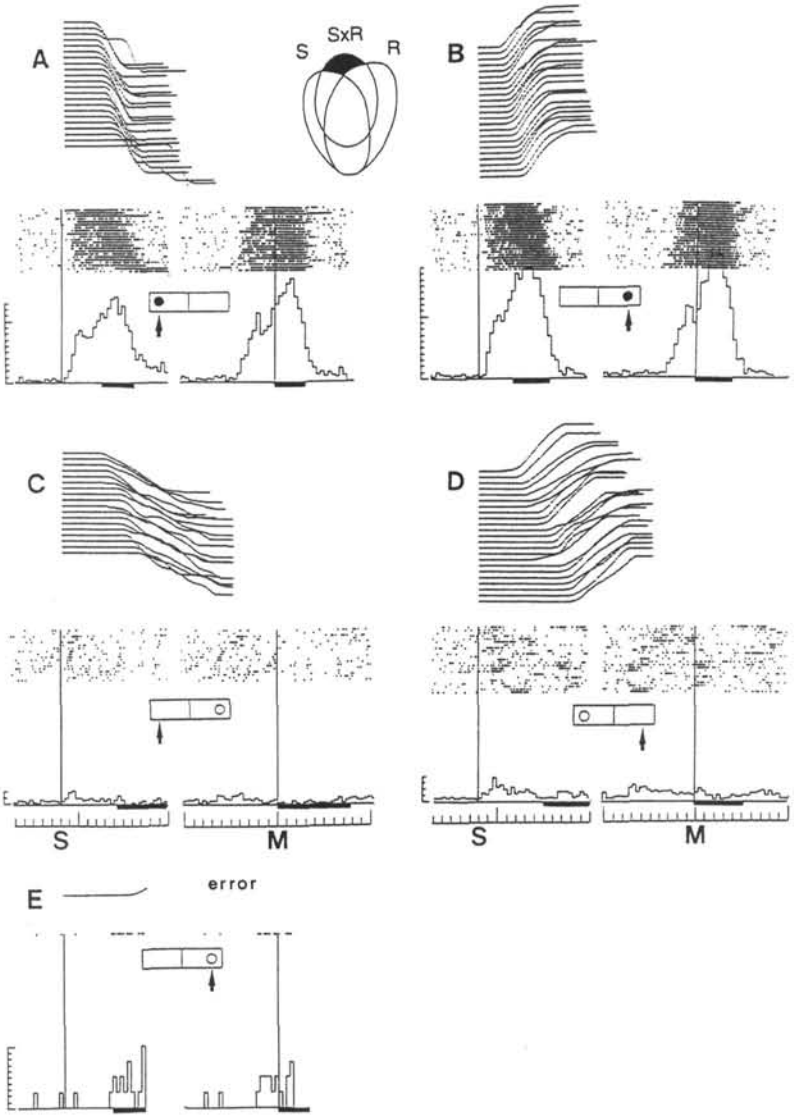

Figure 7. Example of a neuron that was significantly more active during the reaction time period when the stimulus side and movement direction matched, that is, on congruent trials (A and B), than when they mismatched, that is, on incongruent trials (C and D) in Experiment 1. The Stimulus Side × Response Side interaction was the only statistically significant effect shown by the analysis of variance. E: An Erroneous trial in one of the incongruent conditions (i.e., when the stimulus was presented on the right side and the mapping called for a movement to the left side; C). In this error trial, the monkey made a movement to the right, as if it were a congruent trial. Although recording was discontinued when the computer detected an error (i.e., when a movement was made to the wrong side), it can be seen that changes in neuronal activity were similar to those observed during compatible trials (A and B). The presentation was the same as in Figure 5. S = stimulus presentation; M = movement onset. At top, S = stimulus side; S × R = Stimulus × Response Side interaction; R = response side.

As shown in Figure 10A, the class of sensory-related neurons (as defined previously) included a larger percentage of neurons whose activity was exclusively stimulus locked (31%) than of neurons whose activity was either exclusively movement locked (16%) or stimulus and movement locked (21%). These differences, however, were not statistically significant ($\chi^2 = 2.29$). In addition, the class of motor-related neurons included a larger percentage of neurons whose activity was exclusively movement locked (36%) than of neurons whose changes in activity were either exclusively stimulus locked (12%) or stimulus and movement locked (17%). These differences were statistically significant, χ^2 (5, $N = 186$) = 9.36, $p < .01$. Finally, the class of sensorimotor-related neurons included a larger

Table 1
Relationships Between the Functional Properties of Neurons During the RT and MT Periods

	MT								
RT	S	S + S × R	S + R	S × R	S + R + S × R	R + S × R	R	Not significant	Total
S	3	1	2	1	2	3	2	5	19
S + S × R	1	4	1	3	7	3	0	0	19
S + R	0	4	2	4	12	9	4	4	39
S × R	0	1	1	2	3	5	2	4	18
S + R + S × R	1	7	3	3	27	6	1	9	57
R + S × R	1	1	0	1	7	4	5	2	21
R	1	2	4	4	5	7	8	10	41
Not significant	0	4	4	10	8	2	14	21	63
Total	7	24	17	28	71	39	36	55	277

Note. Several neurons were involved in more than one of the main effects (S, R, S × R; cf. Figure 4); for instance, a neuron could be sensitive to both the stimulus side and Stimulus × Response interaction (S + S × R). RT = reaction time; MT = movement time; S = stimulus; R = response.

percentage of neurons whose changes in activity were stimulus and movement locked (62%) than of neurons whose changes in activity were either stimulus locked (56%) or movement locked (48%). These differences were statistically significant, χ^2 (5, N = 339) = 3.88, $p < .05$.

A similar analysis was done on changes in neuronal activity during the MT period. As shown in Figure 10B, the class of sensory-related neurons included a larger percentage of neurons whose activity was exclusively stimulus locked (33%) than neurons whose activity was either exclusively movement locked (12%) or stimulus and movement locked (13%). These differences were marginally significant, χ^2 (5, N = 93) = 3.29, $p < .10$. The class of motor-related neurons included a larger percentage of neurons whose activity was exclusively movement locked (41%) than neurons whose activity was stimulus and movement locked (29%); this class of neurons did not include any cells whose activity was exclusively stimulus locked. These differences were statistically significant, χ^2 (5, N = 225) = 7.95, $p < .01$. Finally, the class of sensorimotor-related neurons included similar percentages, χ^2 (5, N = 348) = 2.66, $p > .5$, of neurons whose activity was stimulus locked (66%), movement locked (48%), or stimulus and movement locked (59%).

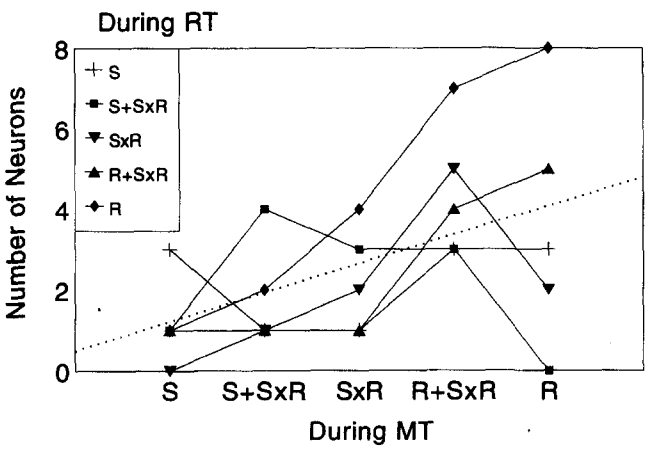

Figure 8. Functional sensory-to-motor shift of neuronal activity from the reaction time (RT) period to the movement time (MT) period in Experiment 1. Each curve represents one type of neuronal activity encountered during RT. The functional shift, during MT, is shown for each type of neuron at the x-axis. The thick line corresponds to the regression through all data, which was highly significant (r = .519, $p < .02$). S = stimulus side; R = response side; S × R = Stimulus × Response Side interaction.

Patterns of neuronal activation in incongruent trials. The automatic response activation hypothesis (i.e., that in incongruent trials, the congruent but incorrect response is initially activated and subsequently aborted before the incongruent but correct response is activated) could be tested by comparing the patterns of neuronal activation associated with the performance of the left and right movements under the two mapping conditions. In particular, the neuronal activity associated with incongruent trials for movements in one direction should at first look like the neuronal activity associated with movements executed in the opposite direction during congruent mapping. Two examples of such a pattern of activation are particularly evident in the histograms of Figure 11. The neuron shown in the upper part of Figure 11 was classified as a sensorimotor-related neuron because it was much more active under congruent (see Figures 11A and 11B) than under incongruent (see Figures 11C and 11D) mapping conditions. Furthermore, as the stimulus-locked and movement-locked data for this neuron show, the beginning of its activation was time locked to stimulus onset, whereas its end was time locked to movement onset. Note that, in congruent trials, the latency of this activation for the stimulus locked data was slightly shorter for flexion (see Figure 11B) than for extension movements (see Figure 11A). When the extension movement was executed in the incongruent condition (see Figure 11C), a small activation, with exactly the same timing as that observed for the congruent flexion movement (see Figure 11B), occurred first and was followed by a second, larger activation whose timing, according to movement start, was similar to that observed for the congruent extension movement (see Figure 11A). Conversely, when the flexion movement was executed in the incongruent condition (see Figure 11D), a small activation, with the same timing as that

observed for the congruent extension movement (see Figure 11A), occurred first and was followed by a second, larger activation whose timing, according to movement onset, was similar to that observed for the congruent flexion movement (see Figure 11B). Note, finally, that the large increase in RT from congruent to incongruent trials was similar to the difference in latency between the first and second neuronal activations in incongruent trials. Similar data for another neuron are shown in the lower part of Figure 11. This neuron was classified as motor related because it was sensitive to both response side and a Stimulus Side × Response Side interaction. To evaluate the proportion of such neurons, one must take into account the fact that neurons whose activity is sensitive to stimulus side are not suitable for verifying the automatic response activation hypothesis. This is because a similar pattern of activity during congruent and incongruent mapping conditions could result either from the automatic activation of the congruent but incorrect response in the incongruent mapping condition or from the fact that the stimulus was presented in the same location. Seventy-four neurons were classified, on the basis of ANOVA results, as being exclusively sensitive either to response side, to an S-R interaction, or to both. This is the population with respect to which it is appropriate to calculate the proportion of "automatically activated congruent neurons." Ten neurons (13.5%) showed a pattern of activation similar to those shown in Figure 11. Note that the changes in activity in these neurons were categorized as stimulus and movement locked on the basis of their timing.

Experiment 2

In the second experiment, we used left–right movements similar to those used in Experiment 1, but this time the relevant stimuli were tones that varied in pitch. The high-pitch tone was mapped onto the movement in one direction, and the low-pitch tone was mapped onto the movement in the other direction. The two tones were randomly presented to the left and right ears. The side of the ear was irrelevant to the task.

Method

Materials and experimental design. The display panel and manipulandum in Experiment 2 were basically the same as those used in Experiment 1, except that only three white LEDs were used and were on continuously. The centrally located LED marked the starting position of the movements; the other two LEDs, located 40° to the left and to the right, served as movement targets. The two loudspeakers were placed 10 cm away from the animal's left and

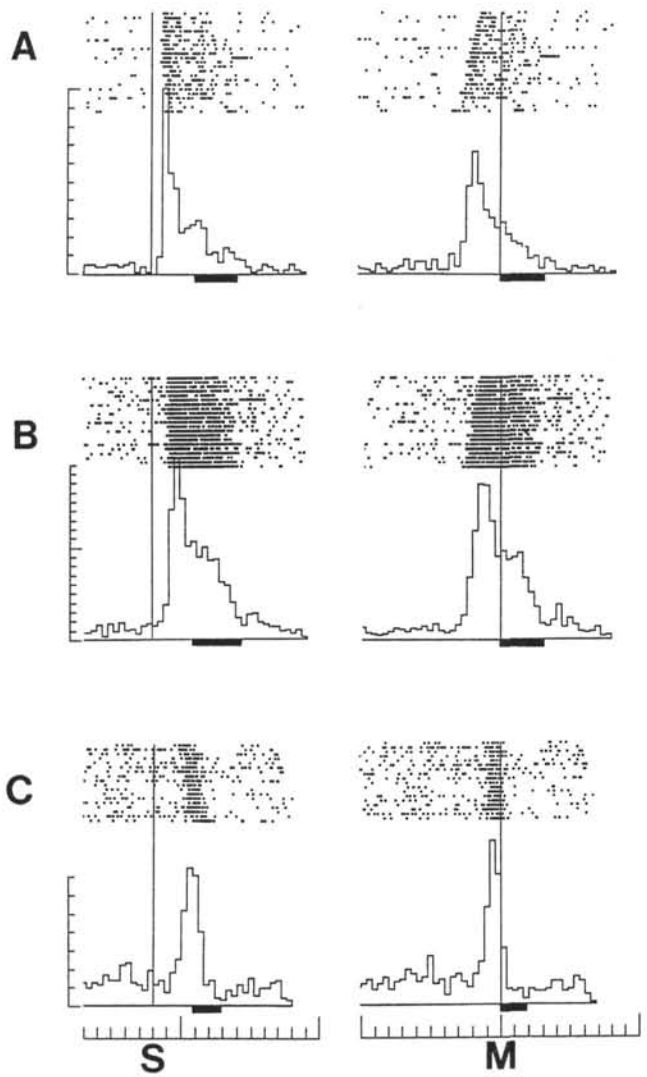

Figure 9. Examples of the three categories of neurons classified on the basis of the timing of their changes in activity in Experiment 1. The presentation is the same as in Figure 5. By comparing the raster displays when aligned with either stimulus onset (left part of the figure) or movement start (right part of the figure), it was possible to determine whether changes in neuronal activation were time locked to stimulus onset (S), movement start (M), or both. A: When neuronal recordings were aligned with S (left side of the figure), the beginning of the change in neuronal activation was time locked to S, whereas when neuronal recordings were aligned with M (right side of the figure), the beginning of the change in activation was not time locked to M but shifted to the left from shortest to longest reaction times (RTs). This neuron was therefore classified as an S-locked neuron. B: When neuronal recordings were aligned with S, the beginning of the change in neuronal activation was time locked to S, but the end of the activation shifted to the right from the shortest to the longest RTs. When these same neuronal recordings were aligned with M, the beginning of the change in neuronal activation shifted to the left from the shortest to the longest RTs, but the end of this activation was time locked to M. This neuron was classified as an SM-locked neuron. C: When neuronal recordings were aligned with S, the beginning of the change in neuronal activation was not time locked to S but shifted to the right from shortest to longest RTs; however, when neuronal recordings were aligned with M, the beginning of the change in neuronal activation was time locked to M. This neuron was thus classified as an M-locked neuron.

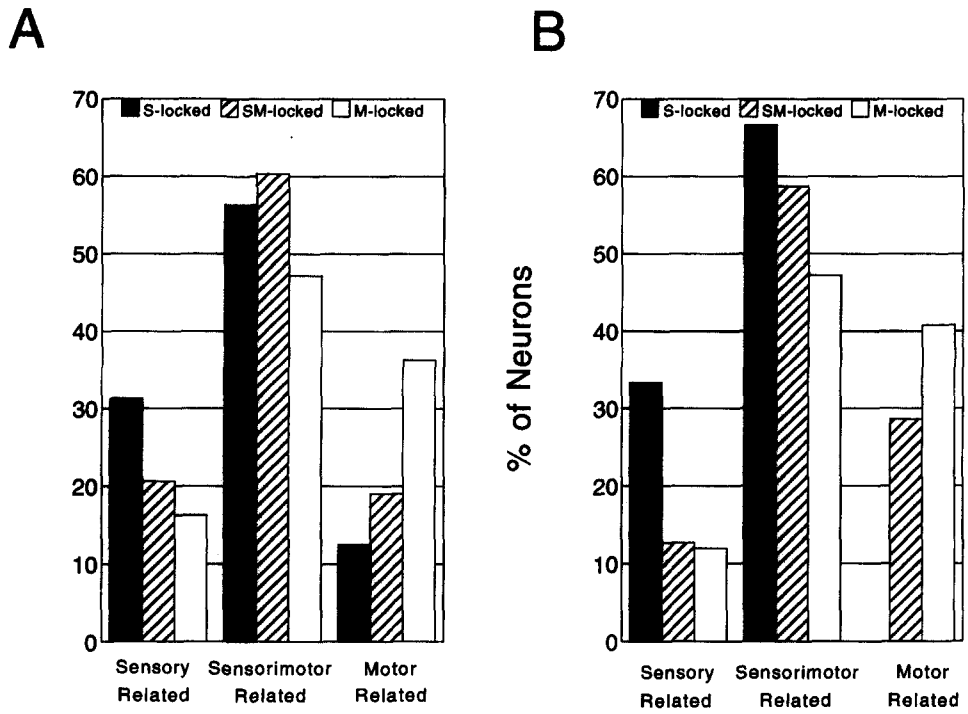

Figure 10. In Experiment 1, relationships between the classifications of neurons based on (a) the sensitivity of their changes in activity during either reaction time (A) or movement time (B) to stimulus side (sensory-related neurons), response side (motor-related neurons), and their interaction (sensorimotor-related neurons) and (b) the timing of these changes in activity according to stimulus occurrence (S-locked neurons), movement onset (M-locked neurons), and both events (SM-locked neurons). The percentages of neurons classified as S-, SM-, and M-locked neurons are shown for each of the three categories of sensory–sensorimotor-related neurons and motor-related neurons. Each of the sums of black columns, hatched columns, or white columns, thus equals 100%.

right ears. A 400- or 1000-Hz tone could be delivered on either loudspeaker and served as the RS.

To start a trial, the monkey had to align the pointer with the starting position and hold it there. After a 2-s delay, either the 400- or 1000-Hz tone was delivered to either the left or the right ear, ending with movement onset. The 400-Hz tone indicated that the animal had to move the pointer toward the left target, and the 1000-Hz tone indicated that he had to make the movement toward the right target. Tones were randomly delivered to the left and right ear, so that the side of the stimulated ear was irrelevant to the performance of the task. A trial was called "consistent" when this irrelevant stimulus matched the direction of the required movement and "inconsistent" when it did not match.

To minimize possible intrusions from the coactivation of antagonist arm muscles during the response movements, monkeys were trained to simply move the handle in the correct direction and overshoot the LED rather than to align the pointer with the LED targets. The monkeys were rewarded by a drop of apple juice when the RT fell below a criterion duration that was progressively reduced during training.

Training lasted about 2 months. During that time consistent and inconsistent trials were blocked during the daily training sessions and alternated from one session to the next. After the monkeys had learned the task under consistent and inconsistent conditions (i.e., when a criterion of more than 80% correct was met in both conditions), consistent and inconsistent trials were randomly intermixed in each daily session, and recordings were made starting on the first day of such mixed sessions. Each recording session included at least 20 trials of each of the four types of trials formed by combining the two types of movement (extension and flexion) with the two conditions of the irrelevant stimulus (consistent and inconsistent). As in Experiment 1, only recording sessions in which the animal performed the task correctly using the 80% criterion for each of the trials were analyzed.

Data analysis. The data analyses were similar to those done for Experiment 1, except for the MTs, which were not recorded in this experiment. In lieu of MTs, we recorded peak movement velocity, which is closely correlated with MT for ballistic movements (Nagasaki, 1989).

Histological control. Animals were anesthetized with ketamine (5 mg/kg im) and sodium pentobarbital and were perfused through the left ventricle with 0.9% NaCl followed by 10% formalin. The brains were removed and suspended in formalin. Later, parasaggital sections (50 μm) were made from the blocks containing the electrode penetrations using a freezing microtome and stained with cresyl violet. This permitted reconstruction of the locations of electrode penetrations (see Riehle & Requin, 1989, for details).

Results

Behavioral results. After Monkey 1 had participated in nine recording sessions, it appeared that, on the basis of the

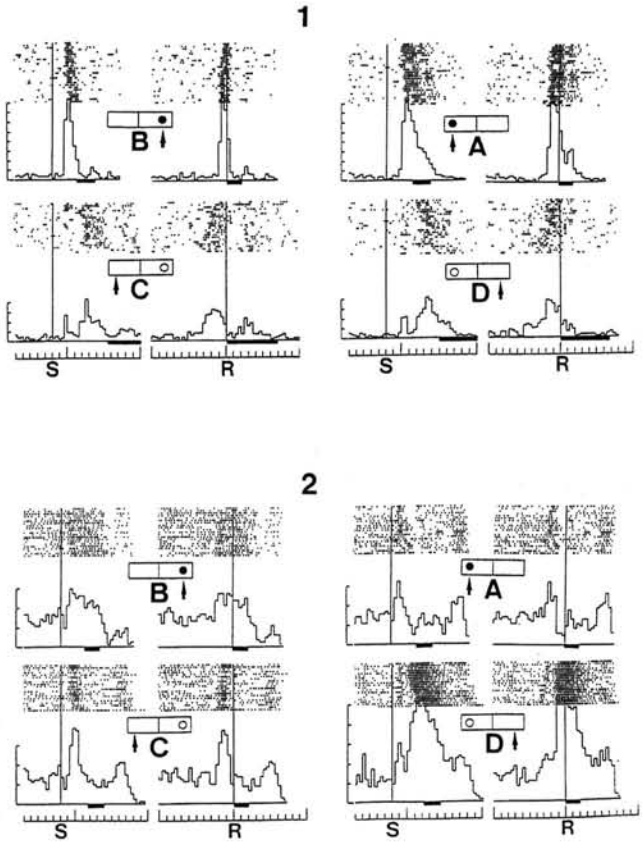

Figure 11. Two examples of neurons (1 = upper part; 2 = lower part) that showed a pattern of activation suggesting that, in incongruent trials, the congruent, incorrect response (R) was activated before the incongruent, correct response in Experiment 1. The presentation is the same as in Figure 5. In incongruent trials (C and D), a brief and small neuronal discharge time locked to the stimulus (S), and of same latency as that of the neuronal activation shown when the movement was performed in the opposite direction during congruent trials (i.e., in D as compared with A and in C as compared with B), first occurred and was followed by a second longer and larger activation.

daily observations made during the recording sessions, no reliable differences in RT were being obtained between consistent and inconsistent conditions. The RTs and peak velocities for this animal were therefore averaged and analyzed. The ANOVA showed that there were no significant effects on RT from either the stimulated ear ($F < 1$) or the movement direction, $F(1, 8) = 5.14$, $p < .10$. Moreover, these two factors did not interact significantly ($F < 1$). Peak velocity was found to depend on movement direction, $F(1, 8) = 276.41$, $p < .001$: Extension was twice as fast (226°/s) as flexion (116.5°/s). However, neither stimulus side ($F < 1$) nor S-R consistency conditions ($F < 1$) had a significant effect on peak velocity. Because Monkey 1 was clearly not behaviorally sensitive to the SRC factor, we stopped the recording sessions and did not further analyze the neuronal activities recorded during these first nine sessions.

Monkey 2 participated in 25 recording sessions. RT and peak velocity data were submitted to a two-factor ANOVA, with stimulated ear and movement direction as factors (cf. Figure 12). RTs were found to be significantly shorter when the tone was presented to the right ear (814 ms) than to the left ear (827 ms), $F(1, 24) = 7.15$, $p < .05$, and for a right (flexion) movement (802 ms) than a left (extension) movement (839 ms), $F(1, 24) = 16.46$, $p < .001$. These two factors interacted significantly, $F(1, 24) = 22.22$, $p < .001$, with RTs being shorter when the side of the stimulated ear and the direction of the movement matched (809 ms), that is, for the consistent condition, than when they did not match (832 ms), that is, for the inconsistent condition. When a similar ANOVA was done on the peak velocity data, the stimulated ear ($F < 1$), the movement direction ($F = 1.81$), and their interaction ($F < 1$) were not statistically significant.

Physiological data. Changes in the activity of 115 MI neurons (cf. Figure 13) in Monkey 2 were analyzed in a manner similar to that in Experiment 1.

Sensitivity of changes in neuronal activity to external and behavioral events. For each neuron, an ANOVA with repeated measures was done on the mean frequency of

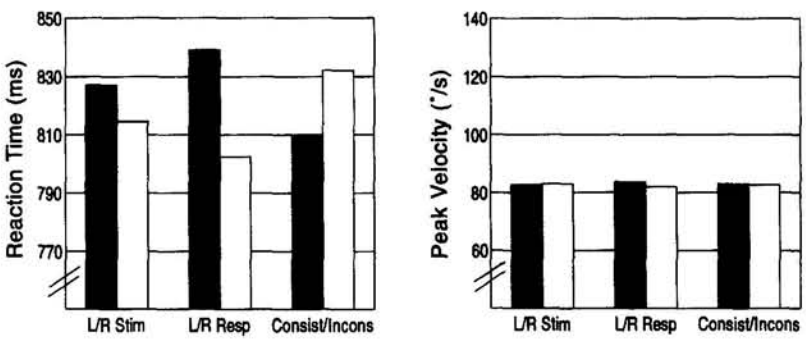

Figure 12. Reaction time and peak velocity of movements, as a function of stimulus (stim) side (left [L] = black columns; right [R] = white columns), response (resp) side (left = black columns; right = white columns), and stimulus–response consistency conditions (consistent [consist] = black columns; inconsistent [incons] = white columns) in Experiment 2.

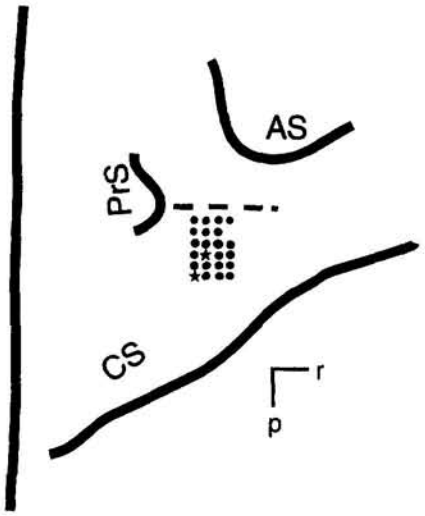

Figure 13. Anatomical location of electrode penetrations in Experiment 2. Stars indicate the sites where neurons whose changes in activity were sensitive only to stimulus–response compatibility were found. r = right; p = posterior; CS = central sulcus; AS = arcuate sulcus; PrS = precentral sulcus.

neuronal activity during the RT period, with stimulus side and response side as factors. Stimulus side had a statistically significant effect ($p < .05$) in 9 neurons (8%), and response side had a statistically significant effect ($p < .05$) in 57 neurons (50%). The Stimulus Side × Response Side interaction (the SRC effect) was statistically significant ($p < .05$) in 9 neurons (8%). Although some neurons were involved in two or three of these effects, the sum of these percentages did not exceed 100% because 52 neurons (45%) were not sensitive to stimulus side, to response side, or to their interaction. This contrasts sharply with the data from Experiment 1. These various populations of neurons are represented in Figure 14A. An example of a neuron whose changes in activity during RT depended only on SRC is shown in Figure 15. In contrast to Experiment 1, there were only 2 neurons for which the SRC effect was the only statistically significant effect.

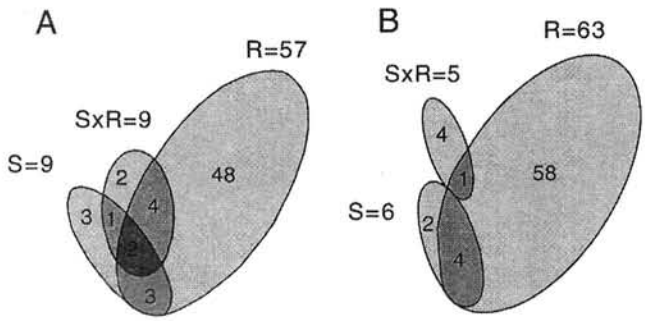

Figure 14. The three classes of neurons whose changes in activity during the reaction time period (A) and the movement time period (B) showed significant effects of stimulus side (S), response side (R), or Stimulus × Response Side interaction (S × R) in Experiment 2. The presentation was the same as in Figure 4.

Although SRC did not affect peak movement velocity, a similar ANOVA was done on the mean frequency of neuronal activity during a 300-ms period after movement onset. Stimulus side had a statistically significant effect ($p < .05$) in 6 neurons (5%), and response side had a statistically significant effect in 63 neurons (55%). The SRC effect was statistically significant ($p < .05$) in 5 neurons (4%), whereas the activity of 46 neurons (39%) was not significant with respect to any of these factors. These various populations of neurons are represented in Figure 14B. As can be seen by comparing Figures 14A and 14B, the size of these neuronal populations during the RT and MT periods is similar. Neither the slight decrease from RT to MT in the number of neurons whose discharge frequency was sensitive to stimulus side (9 to 6), and sensitive SRC (from 9 to 5), nor the slight increase in the number of neurons whose discharge frequency was sensitive to response side (from 57 to 63) was statistically significant.

Timing of changes in neuronal activity. By visually inspecting the raster displays in the same way as was done in the first experiment, changes in the activity of 98 neurons were found to be unequivocally time locked to movement, and changes in 7 neurons were time locked to both movement and stimulus. There were no neurons for which changes in activity could be shown to be time locked only to stimulus onset. Ten neurons could not be classified. A comparison between the two classification procedures similar to that done in Experiment 1 unfortunately could not be done on the data for this experiment. Not only was there no neuronal activity that was exclusively stimulus locked, but the 7 neurons whose changes in activity were time locked to both stimulus and movement were all classified as motor-related neurons. Only neurons whose changes in activity were time locked to movement were distributed in the three classes of sensory-related (4%), motor-related (85.5%), and sensorimotor-related (11.5%) neurons. Consequently, no comparison of the percentages of neurons categorized according to the timing of their activation could be made within these three classes.

Patterns of neuronal activation in incompatible trials. Patterns of neuronal activation associated with the performance of extension and flexion movements in the two SRC conditions were examined to determine whether changes in neuronal activity associated with inconsistent movements performed in one direction would tend to be similar to those changes associated with consistent movements performed in the opposite direction. No such neurons were found. The automatic response activation hypothesis was therefore not supported by these data.

General Discussion

SRC Effects on Behavioral Performance

The RT data of Experiment 1 clearly replicated the pattern of results obtained with human subjects in similar SRC tasks (Kornblum, 1992; Kornblum & Lee, 1995): RT was longer

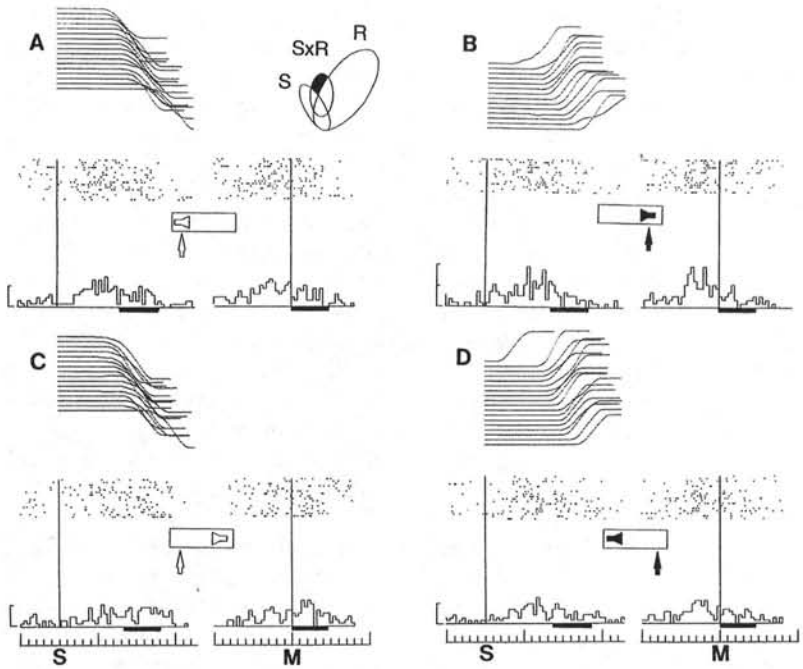

Figure 15. Example of a neuron that was significantly more active during reaction time when the stimulated ear and movement direction were on the same side, that is, consistent trials (A and B), than on opposite sides, that is, inconsistent trials (C and D) in Experiment 2. The Stimulated Ear × Response Side interaction was the only statistically significant effect shown by the analysis of variance. The presentation was the same as in Figure 5. S = stimulus presentation; M = movement onset. At top, S = stimulus side; S × R = Stimulus × Response Side interaction; R = response side.

for incongruent than for congruent mapping. Although this effect was highly significant for both monkeys, it was considerably larger for Monkey 2 (417 ms) than for Monkey 1 (38 ms). This difference may be related to the difference between the 2 animals in learning the task: Monkey 2 took considerably longer than Monkey 1 in meeting the 80% correct criterion.

In both monkeys, the RT was shorter for a right than for a left stimulus and for a left (extension) than for a right (flexion) movement. The effect of stimulus side may be explained by the postural constraints of the task. Both animals performed the task with the left hand. To make the animal more comfortable, the stimulus display and manipulandum were moved toward the animal's left. To get into the starting posture, the animal simply had to straighten his left forearm in front of him. However, this also meant that straight ahead, on the display panel, the animal was facing the right stimulus. The response side effect, which was observed not only on RT but on MT in Monkey 1, might have been related to these postural constraints, although no specific explanation for the faster initiation and execution of extension movements was readily apparent. Previous experiments (Riehle & Requin, 1989, 1995) have shown that this extension advantage is not a consistent finding.

As far as we know, no effects of SRC on MT have been reported in the literature. This may be because most SRC studies in humans have used keypresses as responses and thus MT could not be measured. The large effect of S-R mapping that we found on MT suggests that SRC may be acting on movement execution as well as on response identification. This would be consistent with the processing aspects of Kornblum's DO model (Kornblum et al., 1990), in which an incongruent mapping involves the automatic activation of the congruent, incorrect response. Physiological evidence for the extension of such response activation until movement execution process was reported by Gratton et al. (1988), who showed that in incompatible conditions there was an increase in background electromyogram (EMG) in the muscles involved in performing the incorrect response. Although an EMG was not recorded in our research, the slight oscillations of the potentiometer output during MT (cf., e.g., Figure 7C) strongly suggest that the pointing movements performed in incongruent conditions resulted in the coactivation of antagonistic muscles. To avoid this problem in Experiment 2, the pointing task was changed to a ballistic task that had no accuracy requirements.

In Experiment 2, the RT data for Monkey 2 were similar to those found in human subjects with Type 3 ensembles (see Kornblum, 1992), such as when the irrelevant stimulus dimension overlaps with the response and individual trials are sometimes S-R consistent and sometimes inconsistent. When the irrelevant stimulus dimension is spatial, as it was in Experiment 2, this effect is sometimes referred to as the "Simon effect" (Simon & Small, 1969). The size of this effect (23 ms) we found was comparable to that generally found in human subjects (Simon & Small, 1969; Simon,

Craft, & Webster, 1973). Note that this effect was considerably smaller than the SRC effect found in Experiment 1 when the same animal performed a Type 2 task in which the relevant stimulus feature (stimulus side) was mapped onto movement direction (417 ms). This difference between consistency effects in Type 3 ensembles, and mapping effects in Type 2 ensembles, replicates the results obtained from humans by Kornblum and Lee (1995).

The mean RT of Monkey 2 was, of course, much longer in Experiment 2 than in Experiment 1. We believe that this difference was most likely the result of the task in Experiment 2 being much more difficult than that of Experiment 1. The difference in difficulty between the two tasks was probably due to the arbitrary nature of the S-R association in Experiment 2, where there was no overlap between the relevant stimulus dimension (pitch) and the response (movement direction) and the fact that the S-R mapping in Experiment 1 involved overlapping S-R dimensions. The task in Experiment 2 was much more difficult to learn than that in Experiment 1.

The effects of stimulus side and response side on RT cannot be explained for Experiment 2 in the same way that it was explained in Experiment 1 (i.e., as the consequence of a right–left bias in the postural constraints of the task). First, such an explanation obviously does not apply to the effect of stimulus side because the tones were delivered equally often to each ear. It is possible, of course, that because we did not calibrate the loudspeakers to be physically identical that the stimulus side effect could have been the result of an uncontrolled difference in intensity between the two ears. Second, two factors were confounded in the response side effect (i.e., movement direction and pitch) that were associated with a fixed mapping. Once again, the difference in pitch could have resulted in an uncontrolled difference in auditory stimulus intensity.

Finally, the absence of any Stimulus × Response Side interaction effect on peak movement velocity strongly suggests that the SRC effects found on MT in the first experiment may have been the result of the movement accuracy requirement in Experiment 1, which was omitted in Experiment 2. A possible implication of this finding is that the response selection process, which is traditionally considered to be sensitive to SRC effects, includes not only selecton of the correct direction for the movement but also the ultimate accuracy of the pointing aspect of the movement.

SRC Effects on Neuronal Activity

Neuronal coding of S-R mapping rules. The main finding of Experiment 1 is that about half of the MI neurons that changed their activity during either RT or MT were sensitive to SRC. Of these, a small proportion were sensitive only to SRC. The latter neurons were not involved in either sensory processes after stimulus presentation or in motor processes preceding movement execution. Their only involvement was in the functional linkage that associates sensory inputs with motor outputs.

One could argue that because the congruent and incongruent mapping conditions were signaled by different-colored LEDs, SRC neurons were responding to color rather than mapping rule. However, this is highly unlikely. Auditory (Lamarre, Busby, & Spidalieri, 1983) and visually (Kwan, MacKay, Murphy, & Wong, 1985; Lamarre et al., 1983; Riehle, 1991; Wannier, Maier, & Hepp-Reymond, 1989) induced, signal-locked neuronal changes in activity have been described in the MI. However, these signal-locked neuronal responses were never triggered by the mere physical properties of the stimuli, as they are in primary sensory areas. They were always found after extensive training that had transformed the sensory stimulus into an informative cue containing response-relevant information. It is therefore extremely unlikely that the neurons whose activity changed in connection with the S-R mapping were simply coding stimulus color. First, 53 of these neurons (46%) had their activity time locked to the response compared with 14 (12%) that had their activity time locked to the stimulus. Of the 18 neurons that changed their activity with respect to the S-R mapping exclusively, only 1 neuron had its activity time locked to the stimulus; 11 of these 18 neurons had no temporal relationship with the stimulus. Second, the fact that neuronal activation started with stimulus onset and ended with movement start in 40 (35%) of the SRC-related neurons supports the idea that these neurons are involved in the linkage processes between sensory input and motor output. Finally, when the monkey made errors in one mapping condition (i.e., moved in the wrong direction), the neuronal activation in these error trials was similar to that observed when the same movement was performed in the other mapping condition (cf. Figure 7E), even though the stimulus had a different color. These are all converging lines of evidence that support our assertion that the SRC cells reflect the processing of rule information, not mere sensory information.

Analysis of the changes in neuronal activity during the MT period, which showed that changes in the activity of a large number of neurons were sensitive to S-R mapping, is consistent with the behavioral data showing that SRC had its effects on movement execution processes. In comparing the proportion of neurons in the different categories during the RT and the MT period, we found a gradual shift from the purely sensory to the purely motor end of the continuum via the sensorimotor middle (cf. Table 1 and Figure 8). This functional shift from the RT to the MT period is more easily understandable in terms of populations of neurons than in terms of individual neurons. For example, it would be difficult to explain how one neuron whose activity was sensitive to response side during the RT period suddenly became sensitive to stimulus side during the MT period. It is only when the stochastic distribution of functional shifts within the entire population of neurons is taken into account that changes in neuronal activation from the RT to the MT period support the concept of a progressive buildup of sensorimotor action.

Recall that the percentage of neurons falling into various categories on the basis of the ANOVAs depended on the confidence threshold for the F values. For example, if we

had chosen a significance level of .01 instead of .05, the percentage of neurons in the various categories would have decreased and the percentage of unclassified neurons would have increased. Clearly, any functional categorization scheme for neurons is based on arbitrary criteria that take a continuously varying neuronal population and subdivide it into discrete classes. The underlying neuronal population is probably best characterized as varying along a functional sensory–sensorimotor–motor continuum (Requin et al., 1988, 1992). The large overlap between the neuronal populations whose changes in activity differed according to stimulus side, S-R mapping rule, and response side, respectively (cf. Figure 4), is highly consistent with this concept of a continuous rather than a discrete transformation process of sensory to motor information.

In Experiment 2, although recordings were analyzed only for 1 monkey, thus reducing the sample size of relevant data, the analysis of changes in neuronal activity led to a pattern of results that was not only highly consistent with the RT data but also differed strongly from the pattern found in Experiment 1, in accordance with the different features of the two tasks.

In contrast to the first experiment, in which the three neuronal categories (i.e., neurons sensitive to stimulus side, response side, or stimulus to response side interaction) were of approximately equal size, the main finding of Experiment 2 was that few neurons were sensitive to either stimulus side or SRC, whereas a large number of neurons showed differential changes in activity with movement direction. Such a difference is easily explained. First. recall that the task in Experiment 2 was to associate the pitch of a tone with the direction of a movement: two clearly nonoverlapping S-R dimensions. Consequently, pitch, movement direction, and association rule were confounded factors, so that the class of neurons sensitive to response side probably included neurons that were functionally involved in processing movement direction, as well as neurons responsible for associating sensory input to motor output. Even neurons that were differentially activated merely by pitch cannot be excluded from this category (Lamarre et al., 1983). Second, recall that the effect of the irrelevant stimulus location, the left and right loudspeakers, was evaluated by comparing S-R-consistent with S-R-inconsistent trials and that this SRC effect was found to be weak compared with the SRC effect found in Experiment 1. It would therefore seem unlikely that a large number of neurons were involved in the neuronal mechanism underlying this relatively small interference effect. Nevertheless, the small proportion of neurons whose changes in activity were classified as sensitive to SRC, with two of them being sensitive only to SRC, must be viewed as functionally involved in the interference effect of an irrelevant stimulus dimension.

Relationships between the functional and temporal features of neuronal activity. The two ways of classifying neurons in Experiment 1, the first based on timing and the second on the ANOVA, were found to be consistent, at least at the level of neuronal populations. This consistency greatly strengthens the behavioral significance of the physiological data of Experiment 1. Neither the timing alone nor their amplitude alone could have provided a valid basis for drawing any conclusion about the causal relationships between neural and behavioral processes (see Fetz, 1992; Lemon, 1984; Requin et al., 1992). Together, however, they do.

When the variance of the distribution of changes in neuronal activity for a particular neuron is smaller by aligning these changes to one event (e.g., a stimulus) rather than another (e.g., a movement)—such as when these changes are more strongly time locked to the first than to the second event—one generally infers that the neuron is more functionally involved in processing the first event than the second. Such an inference is correct only if one also assumes that the amplitude and pattern of neuronal activity are constant across trials, which is generally not the case. Similarly, when the amplitude of neuronal activity is systematically and specifically modulated by a behaviorally significant factor (e.g., a stimulus feature or a movement parameter), one generally infers that the neuron is more or less responsible for processing this particular factor. However, such an inference is correct only if one assumes that the amplitude of neuronal activity is measured during a period of time within which this processing is likely to occur, and this is frequently open to question. Therefore, the consistency of our neuronal categorization based on timing on the one hand and the amplitude of neuronal activity on the other serves as converging evidence that validates our inferences about the functional properties of the various subpopulations of neurons.

The functional properties of the three classes of neurons of Experiment 1 can be categorized as follows: The first class is that of sensory-related neurons. These are neurons having the dual property of being primarily sensitive to the stimulus as well as being most often time locked to stimulus onset. These neurons are therefore responsible for the processing of stimulus features. Note, however, that some of these neurons also are involved in the S-R association process. The second class is that of sensorimotor-related neurons, which also have a dual property. First, they are primarily sensitive to both the stimulus and the response or their interaction. Second, they are most often time locked to both stimulus onset and movement start. These neurons are therefore responsible for processing the S-R linkage (i.e., the selection of the appropriate response given the stimulus, in accordance with the mapping rule). A striking feature of these neurons is that they most often show sustained activation during the entire stimulus-to-movement period. The third class is that of motor-related neurons. These are neurons with the dual property of being primarily sensitive to the response as well as being most often time locked to movement start. These neurons are therefore responsible for processing the response parameters. Note that some of these neurons also are involved in the temporally preceding S-R association process.

This classification highlights the fact that a strict one-to-one mapping between these neuronal populations and the three serially organized processing stages (classically thought to be the minimal subdivision of sensorimotor information processing) cannot be verified by our data. Not only do these

neuronal populations overlap functionally, as the results of the ANOVAs show, but they overlap temporally as well, thus supporting the concept of continuous, rather than discrete, processing of sensory input to motor output, as already suggested by the results of a previous experiment (Miller et al., 1992).

Neuronal correlates of an activation of the incorrect response. Some neurons in Experiment 1 showed the pattern of activation predicted by the automatic response activation hypothesis for incongruent mapping. One could argue that because only a small proportion of neurons (13.5% of the selected neurons) showed this pattern of activation, and because it was observed in only a small proportion of trials (see, e.g., Figures 11C and 11D), it is, at best, weak evidence in support of the automatic response activation hypothesis. Recall, however, that only neurons that showed a clear difference in latency between their activation for congruent and incongruent trials and left and right responses were selected (cf. Figure 11). This was done to obtain unequivocal identification of the two successive neuronal activations corresponding to the congruent and the incongruent responses. Given that the monkeys made few errors (80% was the criterion, but usually the monkeys made many fewer errors), these data are consistent with the automatic activation hypothesis. That is, if it had been the case that a large proportion of neurons had displayed large activation of the congruent, erroneous response on a large proportion of incongruent trials, then the monkey would undoubtedly have executed this erroneous movement on a relatively large proportion of such trials. However, the error rate in Experiment 1 was low. Furthermore, the necessarily weak activation of the congruent, erroneous response in the incongruent mapping (if strong, the automatically activated response would be performed) may not have resulted from mere activation but may have been the result of inhibitory control processes that prevented overt responses and intervened at earlier processing stages, hence in cortical areas other than MI. The data presented here also are compatible with those of Coles et al. (1985) and Osman et al. (1992), who recorded event-related potentials in humans during similar SRC tasks. In incongruent mapping, the amplitude of the lateralized readiness potential that was observed initially on the hemisphere ipsilateral to the correct response was considerably smaller than that of the lateralized readiness potential recorded later on the contralateral hemisphere.

The proportion of these "automatically activated congruent neurons" also may have been underestimated by the exclusion of neurons that were sensitive to stimulus side, a factor that might be confounded with a possible automatic activation of the consistent response in the incongruent mapping. These two factors can now be disentangled in light of the preceding discussion in which we argued that it was unlikely that SRC-related neurons were responding to the mere color of the LEDs. That is, if the functional meaning of the signal-related changes in neuronal activity found in MI is not to code the physical properties of stimuli but to provide information to the motor system about the movement to be performed on the basis of stimulus location, which is the congruent response, then they would cue the incorrect response in the incongruent mapping condition. Given this argument, the population of neurons sensitive to stimulus side may be considered as expressing the automatic activation of the consistent but incorrect response in the incongruent mapping condition. This would have increased the number of neurons to 144 in Experiment 1, that is, those neurons that were sensitive to stimulus side ($n = 134$) plus the 10 neurons whose activation pattern was similar to those shown in Figure 11. In other words, this would be 52% of the whole neuronal population. In Experiment 2, in which only 9 neurons that were sensitive to stimulus side were found, this proportion would remain small (8%). Such a difference between the two experiments leads one to the hypothesis that the automatic activation of the consistent response would be responsible for the S-R mapping effect when a relevant stimulus feature is manipulated (Type 2 ensembles in Kornblum's taxonomy), a mechanism that would not be at work when an irrelevant stimulus feature is manipulated (Type 3 ensembles of Kornblum's taxonomy). Note, however, that such a hypothesis is weakened because the stimuli whose relevant (Experiment 1) or irrelevant (Experiment 2) feature was mapped onto the responses, respectively, were presented in a different sensory modality, visual in Experiment 1 and auditory in Experiment 2; previous experiments have shown that the neuronal activity of MI was less influenced by auditory than by visual inputs (Lamarre et al., 1983).

Significance of Results in Current Conceptions of Sensorimotor Systems

In Experiments 1 and 2, we examined neurons in MI that appeared to participate in or to be responsible for coding the S-R mapping rules (i.e., neurons that might be considered as primarily involved in associating stimulus inputs with motor outputs). These types of neurons were mostly found in cortical association areas that are generally viewed as the sites for sensorimotor integration (for reviews, see Andersen, 1987; Stein, 1989). This finding adds support to the current efforts to reexamine the classical views of the relationships between brain structures and behavioral functions, especially the concept of a one-to-one mapping between cortical areas and functions (Requin et al., 1992).

The assignment of cortical association areas to sensorimotor processes had its origins in the influential work of Mountcastle, Lynch, Georgopoulos, Sakata, and Acuna (1975). Mountcastle et al. attributed to the posterior parietal cortex (PPC) not only the role in information integration from different sensory modalities but also a "command function" for the initiation of motor and oculomotor behaviors. Even though this view was challenged (for reviews, see Lynch, 1980; Andersen, 1987), the involvement of PPC in the earliest stages of motor actions was subsequently confirmed when sensorimotor neurons, that is, neurons that modified their activity in relation to both stimulus presentation and movement execution, were discovered in area 5 (Crammond & Kalaska, 1989; Seal, 1989; Seal & Commenges, 1985; Seal, Gross, & Bioulac, 1982) as well as in area 7 (Andersen, 1987, 1989; Andersen, Essick, & Siegel,

1987). However, such two-component neurons (as had already been observed in the auditory cortex by Vaadia et al., 1982) also were recently found in the PM cortex (Crammond & Kalaska, 1994; Riehle & Requin, 1989; Rizzolatti et al., 1988) and in MI (Miller et al., 1992; Riehle & Requin, 1989), thus precluding sensorimotor association as a privileged function of PPC. The results of our research confirm not only the presence of such neurons in MI, but also their specific involvement in sensorimotor processes. The activation of such neurons has been shown to be the result of rules that associate stimuli with responses rather than stimulus properties or movement properties in isolation. The neuronal structures interfacing sensory inputs and motor outputs are probably widely distributed across a large part of the cerebral cortex (Requin, 1992; Requin et al., 1988, 1992).

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