

Divergent Movement of Adjacent Whiskers

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Sachdev, Robert N. S., Takashi Sato, and Ford F. Ebner. Divergent movement of adjacent whiskers. *J Neurophysiol* 87: 1440–1448, 2002; 10.1152/jn.00539.2001. The current view of whisker movement is that ~25 whiskers on each side of the face move in synchrony. To determine whether whiskers are constrained to move together, we trained rats to use two whiskers on the same side of the face in simple behavioral tasks and videotaped the whiskers during the task. Here we report that the movement of adjacent whiskers is usually synchronous but can diverge: 1) the distance between whiskers can vary dramatically during movement; 2) one whisker can move while the second one remains stationary; 3) two whiskers can simultaneously move in opposite directions; and 4) one whisker can be maintained in contact with an object while the other is retracted and protracted. The frequency of whisker movement during the task falls within the previously reported range for rats whisking freely into air or performing roughness discrimination with their whiskers. Our data also suggest that whisker movement can be divided into three distinct phases: protraction, retraction, and a measurable delay between these movements. We conclude that, although whiskers often move in concert, adjacent caudal whiskers can be moved independently of each other.

INTRODUCTION

Two sets of muscles are typically associated with whiskers: intrinsic muscles attached to each whisker and extrinsic muscles that have their origin outside the whisker pad (Dorfl 1982). The stereotyped simultaneous movement of the approximately 25 whiskers, known as whisking is thought to be produced by contraction of intrinsic muscles (Carvell and Simons 1990; Dorfl 1982; Wineski 1983). According to this model, contraction of a single intrinsic muscle moves a single whisker forward (protraction), while retraction to a resting position occurs passively due to elasticity of the tissue (Dorfl 1982). Few studies have questioned this model or examined whether the whiskers are constrained to move in synchrony. Two possibilities exist. One possibility is that adjacent whiskers are constrained to move together because all intrinsic muscles contract in the same instant, or because extrinsic muscles that move the whisker pad en masse play an important role in all whisker movements. A second possibility is that the synergy between intrinsic muscles for each whisker (and between extrinsic and intrinsic muscles) can be dynamically modified, and whiskers can move independently.

Anatomical evidence suggests that independent control of single whiskers is possible because each intrinsic muscle forms a sling around the base of a single whisker (Dorfl

1982). Both ends of the muscle insert into the superficial connective tissue surrounding the whisker follicle caudal to it (Dorfl 1982). Studies of the facial motor neuron projection to the whisker pad are inconclusive about the separate facial motoneuron innervation of each follicle muscle. But these studies suggest that distinct groups of motoneurons innervate distinct whisker rows (Dorfl 1985; Klein and Rhoades 1985; Semba and David Egger 1986; Watson et al. 1982). Electromyographic (EMG) studies of the whisker pad are of little help in resolving this issue because the EMG signal from the whisker pad reflects the summed activity from many intrinsic muscles (Carvell et al. 1991; Fee et al. 1997; Semba and Komisaruk 1984). Nevertheless, according to the motor unit concept, motoneurons in the facial nerve nucleus are assumed to exclusively innervate muscle fibers in single intrinsic muscles (Creed et al. 1932).

Observation of whisker movement provides an additional method to examine the synchrony of whisker movements. Divergent movements of adjacent whiskers during a task would provide evidence that whiskers are not constrained to move together. Earlier studies have focused on measuring whisking frequency during sniffing or during large whisks into the air (Bermejo et al. 1996; Hutson and Masterton 1986; Welker 1964) or when the animal uses its whiskers to discriminate between surfaces (Carvell and Simons 1990, 1991, 1996). Several studies have examined the position of multiple whiskers during whisking and contact (Carvell and Simons 1990; Wineski 1983). The work presented here differs in important ways from previous behavioral studies; the head is restrained, the task is purely whisker contact dependent, and contact itself, not discrimination of surface texture, triggers a reward. In the present studies whisker contact was detected by a sensitive contact detector (Bermejo and Zeigler 2000), with and without a conditioning cue. Our results show that two long caudal whiskers often move in concert, but are not constrained to move together.

METHODS

Methods for head restraint and general conditioning of the animal have been described earlier (Bermejo et al. 1996; Sachdev et al. 2000). Briefly, six adult male Long Evans rats were obtained from an in-house breeding colony. Rats were handled daily for a week and then placed on a diet that brought them to 80% of their free feeding weight. Each day, rats were acclimated to restraint in a loosely fitting cloth bag. Restrained rats were placed in a plastic tube and fed

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chocolate milk. Once rats began drinking ad-lib chocolate milk that was available during the 20- to 30-min training session (5–10 days, gaining ~15 g in a single session), they were considered ready for head-restraint surgery.

Animals were anesthetized with Ketamine/Xylazine (90 mg/10 mg per kg). Small holes were made in the skull; three over the cerebellum, and two to three over the olfactory bulbs. Holes in the skull were tapped, and blunt tipped screws were inserted. A head post was fixed over the cerebellum using dental acrylic. Animals were allowed to recover from the surgery. A week after surgery, animals were acclimated to body restraint combined with head restraint. Once head restrained, rats could only obtain chocolate milk by protracting their whiskers until they touched a contact sensor.

Training paradigms

Animals were trained on one of two paradigms: a self-initiated movement paradigm designed for relatively naïve animals and a cue-initiated movement paradigm designed for extensively trained animals. These training paradigms were designed to examine the effect of task parameters on how whiskers are moved and used. One was a simple self-initiated whisker contact and the other was a go-cue-initiated whisker contact. In the simple task, animals ($n = 4$) were trained to protract their untrimmed whiskers to touch a sensor, activating a circuit that released chocolate milk. In this paradigm, the only constraint on the animal was a 2-s period after a reward when no further rewards could be obtained. This constraint ensured that a single contact was rewarded even though multiple contacts often occurred. The interval between rewards prevented any licking/chewing or related artifacts from eliciting rewards for the animal. Animals learned this task in 2 days.

Animals ($n = 2$, D1 and D2 whisker intact) trained to do the cued task required extensive training (45 days). In the first days of training, a light-emitting diode (LED) and a sound (white noise) were turned on for 5 s. Any contact that reached threshold while the cues were on elicited a reward. Intertrial intervals were 1 s. By the end of training, intertrial intervals were randomized between 3, 4, and 5 s. Rats were expected to complete movement and contact 1–2 s after cue onset. Once the animals performed the task well, whisker contact with the sensor in the intertrial intervals (when light and sound cues were off) was negatively reinforced by air puffs on the nose. Randomizing trial duration and intertrial intervals and delivering negative reinforcement for incorrect contacts ensured that the animal continued to attend to the task.

Piezo contact sensor

The contact sensor (a piezo electric element) has been described in detail previously (Bermejo and Zeigler 2000). When whiskers contacted the edge of the sensor, an analog voltage was generated. The analog output from the sensor was amplified and fed into a CED interface (Cambridge Electronic Design, London) and digitized. No attempt was made to quantify force or contact duration from the output of the sensor because the sensor oscillates on contact. Thresholds were set 25% greater than the noise (Fig. 1, A and B). Even though the piezo sensor was very sensitive, only approximately 70% of all intentional contacts were detected.

The contact detector was positioned at different points in the two tasks. In the cued task, the sensor was placed 1–2 cm from the typical resting position (see Figs. 2 and 3, for resting position and point of contact) of the whiskers. Animals could increase or decrease the distance between their whiskers and sensor by retracting or protracting whisker before the final protraction that resulted in contact. In the self-initiated task, the sensor was placed near the tip of the nose requiring a distinct movement from natural resting position of the whiskers. However, in both tasks, the final protraction before contact

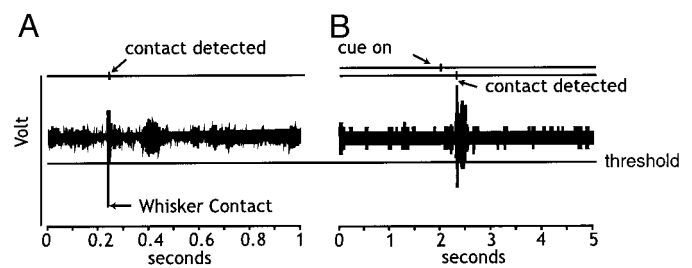


FIG. 1. Detection of contact. A: digitized output from the piezo contact sensor showing that whisker contact during self-initiated protraction causes a transient deflection in the amplified analog output. The deflection in the output was detected because it crossed threshold. B: 5 s digitized output from the piezo contact sensor showing the cue initiated contact. It takes 280 ms after cue onset for the rostral whisker to contact the sensor. Note that the sensor responds transiently to contact. When the transient output crosses threshold, the animal gets a reward.

could occur from any point, even a point <0.5 cm from the contact detector.

Whisker trimming

Whiskers were trimmed in such a way that only two whiskers, C1-C2 or D1-D2 (2 cue-initiated and 2 self-initiated) or D1-Delta, were long enough to make contact with the sensor. In two of four animals in the self-initiated movement group, whiskers that were used in contact were trimmed to 4-cm length. Additionally, whiskers that were not used in the contact task were left sufficiently visible where they could serve as fiducials (on some trials) for the position/activity of whiskers in that row or arc (see Fig. 2). In the animals trained with go-cues, all whiskers except for the two used in the task were trimmed to the fur. In all animals, contact with the sensor occurred at the shaft of the whisker (1.5–2.5 cm from the base).

Data analysis

A Redlake motionscope, generously provided by Dr. Ken Catania (Vanderbilt) was used to record whisker movement to videotape. Whisker movement was recorded at 250 frames/s and transcribed to videotape at frame rates of 5–10 frames/s. This provided adequate temporal and spatial resolution to determine onset and end of whisker movement. Very fine movements were nevertheless excluded from the analysis. The movement of each whisker was followed before during and after contact. Movement onset times, movement direction, contact onset times, and end of contact were noted for each whisker.

The number of protractions and retractions and the beginning and end of the movement were noted. Times when only one of two whiskers moved were also noted.

Examination of brains

Animals were killed with an overdose of anesthetic at the end of each experiment. Animals were perfused with saline, followed by 4% paraformaldehyde, and were examined for damage from the surgical implantation of screws and head posts. None of the brains showed signs of trauma from surgical implantation.

All methods were approved by the Vanderbilt University animal care committee and were in accordance with National Institutes of Health approved procedures (National Institutes of Health publication No. 85-23).

RESULTS

Visual observation of the videotaped whisker movement showed that adjacent whiskers moved together most of the time. However, there was clear evidence that whiskers could

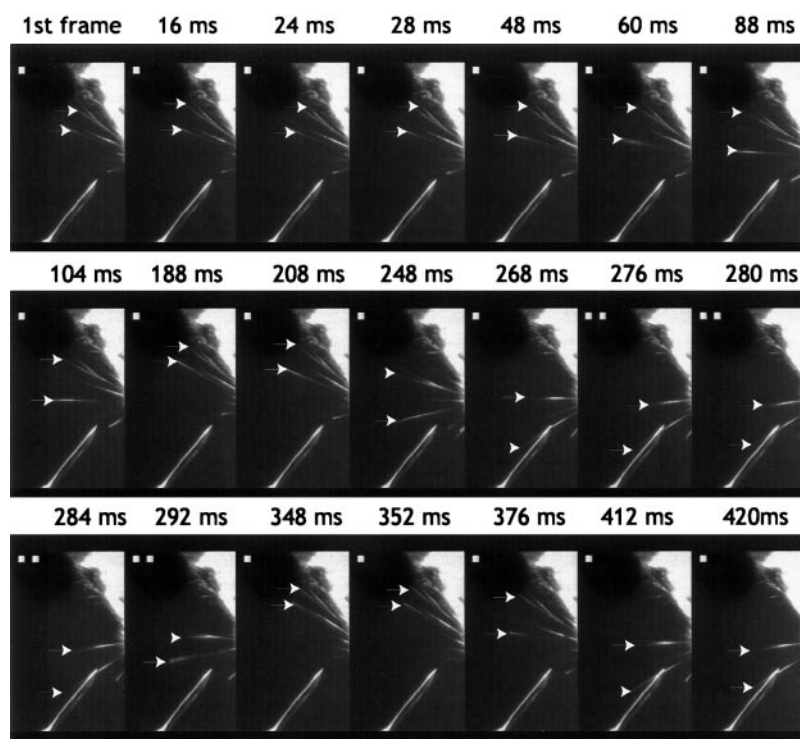


FIG. 2. Sequence of whisker movements showing changes in position of adjacent whiskers. Note that when fully retracted (1st frame) whiskers are closer together than during movement. For example, the position of the D1 and D2 whiskers relative to each other is very different at the 1st frame and 60 ms later. The D1 whisker is a doublet, a replacement whisker is emerging. The D2 whisker makes contact with the sensor at 276 ms. The C1 whisker and other trimmed whiskers can be seen around the D1 and D2 whiskers. These whiskers serve as fiducial markers for the position of whiskers throughout the whisker pad. Between the 1st frame and 88 ms later, the D2 whisker moves more relative to both the D1 and the C1 whisker. In these sequences, protraction occurs between 24 and 104 ms, 208 and 276 ms, and from 376 ms onward. Retraction occurs between 108 and 188 ms, and 288 and 352 ms. These frames are taken from an animal trained in the self-initiated task. The arrows point to the D1 and D2 whiskers.

simultaneously move in opposite directions, move at different rates, or move individually. Observation also suggested that whisking sequence could be broken into three measurable phases: protraction, retraction, and the interval between these movements, which could include contact.

Number of movements

In the self-initiated task, 55 contacts including movements 250 ms before and after contact were included in the analysis ($n = 332$, 170 protractions and 162 retractions).

Twenty-four successful trials were included from the cued task. In these trials the animal obtained a reward within 1 s after cue onset. Forty-four contacts, involving 308 movements (166 protractions and 142 retractions), were observed between the 200 ms before cue onset and 200 ms after contact ended.

In 84 additional movements, adjacent whisker movement diverged (20 times in the self-initiated and 64 times in the cued task). All types of divergent movements [a single whisker moving, simultaneous movement of 2 whiskers in opposite direction, and retraction of the caudal whisker during contact by the more rostral whisker (Figs. 2–6)] were observed in both groups of animals.

In 110 of the total 640 (from the self-initiated and cued task), movement-onset or movement-end times were different for the 2 whiskers (Fig. 7).

Comprehensive temporal data from 640 movements where adjacent whiskers moved together most of the time is presented in Figs. 8–11.

Divergent whisker movement

One indicator of divergent movement was the increasing distance between adjacent whiskers during movement. Whisker movement sequences in Fig. 2 illustrate the relative position of adjacent whiskers during protraction, retraction, and

contact. At full retraction, the whiskers were close to each other. As whiskers protracted, the angle between whiskers increased. The relative position of whiskers changed most at the onset and end of movements. Two examples of the relative position of whiskers during whisking were drawn from video tape (Fig. 3, *top*). The distance between the whiskers was measured and plotted (Fig. 3, *bottom*). During one sequence of movements that lasted for <500 ms, the separation between

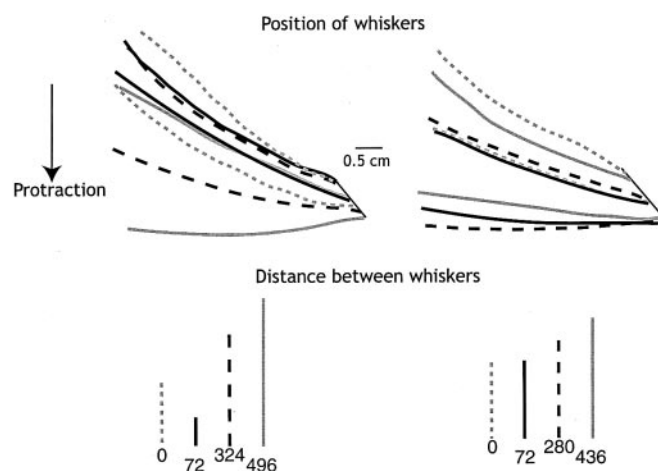


FIG. 3. Examples of changes in relative position of whiskers during movement in the cue initiated task. The D1 and D2 whisker are drawn from frames such as those shown in Fig. 2. The position of the 2 whiskers in 4 frames is shown here. The *left panel* shows that from 0 ms (dashed gray lines) to 72 ms (black lines), the distance between whiskers decreases. The caudal whisker was protracted while the rostral whisker was retracted (compare positions of dashed gray whiskers to position at black, and compare in the *bottom panel* the length of gray line to the black). The distance between whiskers increases as the whiskers are protracted from their position at 72 ms to their position at 496 ms. Similar but less dramatic differences in relative position of D1 and D2 whisker are shown on the *right*.

whiskers varied greatly from ~ 0.3 to 2 cm. These data show that the relative position of adjacent whiskers can change during a single movement. Differences in rate of movement of the adjacent whiskers, differences in timing of movement, or differences in both could contribute to this effect.

For the purposes of this study, if both whiskers moved in the same direction, the movements were considered synchronous even if it appeared that the position of the whiskers relative to each other changed during the movement. An extreme example of temporally distinct movement was the movement of one of the two whiskers; one whisker moved without any noticeable movement of the adjacent whisker (Fig. 4). The whisker that remained stationary was not impeded in its movement by the contact sensor or any other object. The average single whisker movement duration was 24 ± 2.4 ms (mean \pm SE, $n = 60$). These movements could involve either whisker and could involve either a protraction or a retraction. Typically, single-whisker movement occurred in clusters, as if on particular trials the animal adopted a strategy of moving single whiskers.

Whiskers could move simultaneously in opposite directions (Fig. 5). These movements covering 12–24 ms ($n = 7$) occurred when whiskers changed direction rapidly. Typically, the caudal whisker was still being retracted as the rostral whisker reversed direction and was protracted. The caudal whisker subsequently stopped and joined the rostral whisker in protraction.

These observations show that the large caudal whiskers can be moved independently of each other.

Divergent movement at contact

The only requirement of these tasks was that the animal make contact with the sensor and that this contact cross threshold to elicit a reward. Rats appear to develop strategies that increase the likelihood of rewards. In an earlier study, this could involve multiple whisker contact (Sachdev et al. 2001). In the present study all contacts were by a single “rostral” whisker. The alternative strategy for eliciting a reward in-

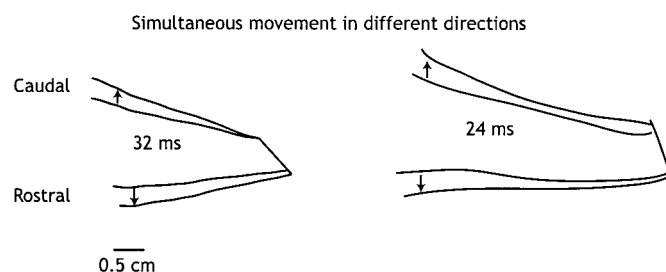


FIG. 5. Examples of movement in opposite directions. Movements are small and tend to occur as the animal changes direction of movement or brings whiskers to a stop. Arrows point to the direction of movement.

involved moving the caudal whisker alone while the rostral whisker maintained contact (Fig. 6). The movement consisted of making contact with the rostral whisker while the caudal whisker protraction was continued. The caudal whisker protraction while the rostral whisker was in contact was not surprising; this movement could be a simple continuation of protraction (that for the caudal whisker is unimpeded by the contact detector). Subsequently, however, while the rostral whisker maintained contact, the caudal whisker alone was retracted. The caudal whisker then completed a rapid retraction, protraction, retraction cycle, even as the rostral whisker maintained contact. This strategy successfully elicited a reward in 8 of 10 contacts where rats adopted this strategy.

Temporal differences in movement of adjacent whiskers

Divergent movement of whiskers could be explained by systematic temporal differences in contraction of the rostral as opposed to caudal intrinsic muscles. It is possible, for example, that a set of intrinsic (or extrinsic) muscles contract and relax first, and therefore move the caudal whiskers before the rostral (or rostral whiskers before the caudal). This possibility was not supported by the data. Most of the time adjacent whiskers begin movement in the same 4-ms time frame.

However, in addition to clear cases where whiskers moved

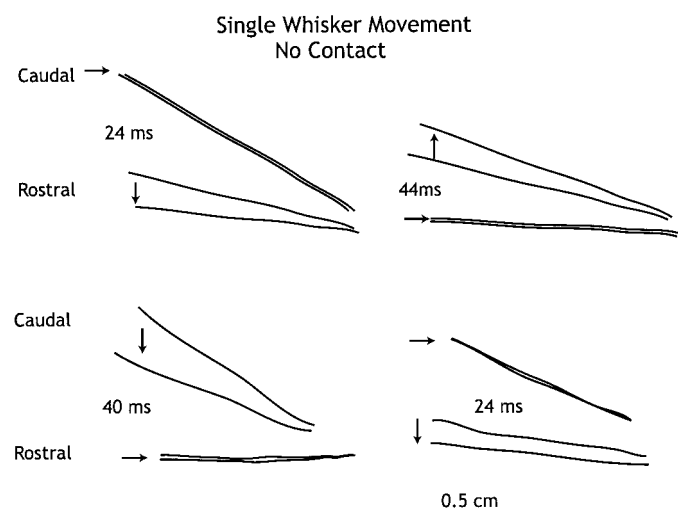


FIG. 4. Examples of single whisker movement. Single whiskers could be protracted or retracted (top left panel) without any apparent movement of the adjacent whisker. In all of these examples 1 of the 2 whiskers did not move even though its movement was not impeded by contact with an object. Arrows point to direction of movement. Horizontal arrows point to stationary whisker.

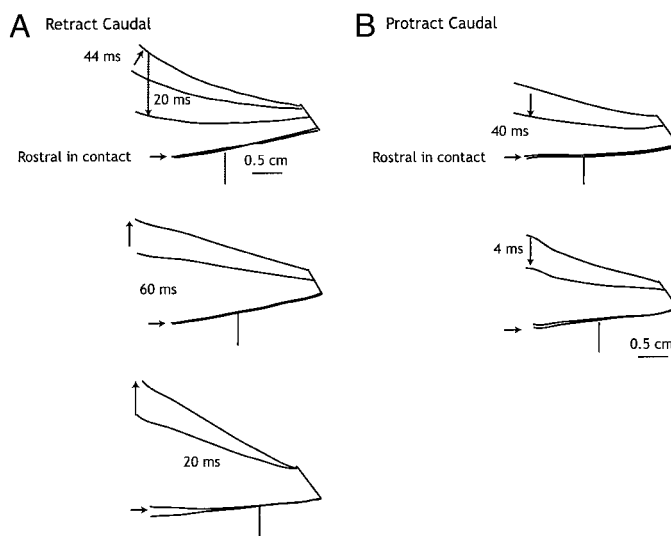


FIG. 6. Examples of caudal whisker moving during contact by rostral whisker. The caudal whisker can be retracted alone (A) while the rostral whisker maintained contact with the detector. Or the caudal whisker is protracted even after contact (B). Arrows point in direction of movement. Horizontal arrows point to whiskers in contact that do not move.

in different directions, or moved alone, some movements diverged only at the beginning or end of the movement. An obvious case was the moment of contact. The rostral whisker contacted the sensor and stopped moving while the caudal whisker either came to a stop or kept moving (Fig. 6B). In 38 contacts (of 95), both whiskers came to a stop simultaneously. The rest of time at contact and at the end of 53 other protractions that did not involve contact an average time difference of 12 ms was observed (Fig. 7, *top right*) with the rostral stopping earlier. Frequently, the caudal whisker began retraction 12 ms before the rostral whisker (Fig. 7). The beginning of protraction and the end of retraction also had similar temporal differences.

Parameters of whisker movement

TIMING OF MOVEMENT RELATIVE TO CUES AND CONTACT. Several studies have examined whisking frequencies during contact tasks (Bermejo and Zeigler 2000; Carvell and Simons 1990; Fee et al. 1997; Nicolelis et al. 1995), but none have reported the timing of protraction or retraction relative to contact. Cue-elicited whisker contact occurs 213 ± 18.5 ms after the cue onset. Cue onset elicited a general increase in whisker movements, but the movements occurred at variable times relative to cue onset (Fig. 8A, *left histogram*). From trial to trial the movement onset latency was variable, and this is evident in the cue-triggered histogram. The number of both protractions and retractions increased when the cue turned on (Fig. 8A, *top histograms*). As seen in the histogram, protraction increased (Fig. 8A, *middle*) after cue onset, and retraction increased approximately 150 ms after cue onset (Fig. 8A, *right*).

There was slightly more temporal consistency (from trial to trial) when the same movements were aligned to contact (Fig. 8A, *bottom*). Protraction increased in the 8–40 ms before

contact. The average protraction duration that resulted in rewarded contact was 32.2 ± 4.0 ms. Retractions increased after contact. Contact duration was 46.2 ± 7.0 ms for cue-initiated movements (Fig. 9).

The timing of movement in the self-initiated group of animals was different from the timing of movement in the cue-initiated animals (compare Fig. 8, A with B). In the self-initiated group, number of protractions increased 40–80 ms before contact occurred. The mean protraction duration before contact was 53.6 ± 2.8 ms. Protraction increased 50 ms after contact. Self-initiated contact lasted 21.8 ± 2.8 ms (Fig. 9). Retraction began almost immediately after contact, peaking 20 ms later. There was another series of retractions nearly 100 ms after contact.

These results illustrate that the timing and duration of whisker movement can be modified by training.

DURATION OF PROTRACTION AND RETRACTION. The frequency of whisking is determined by the dwell time in three phases: protraction duration, retraction duration, and the interval between these movements, sometimes including contact. Previous studies have reported the frequency and amplitude without reporting the duration of each phase (but see Gao et al. 2001).

Changes in whisking frequency could occur by modulating each one of these phases. In this study, it was possible to measure the duration for 640 movements (332 in self-initiated, 308 cue-initiated). The time between the end of one movement in one direction and the beginning of movement in another direction were measured, in 336 intervals between protraction and retraction. Intervals between two movements in the same direction (protraction followed by protraction and retraction followed by retraction) were excluded.

For the animals producing cue-initiated movements, the protraction duration was 32.6 ± 1.8 ms, and the retraction duration was 29.0 ± 1.6 ms (Fig. 10A). In the self-initiated movements, the duration of protraction and retraction was 51 ± 1.8 ms and 40 ± 1.7 , respectively (Fig. 10B). The interval between the end of protraction and beginning of retraction (and the end of retraction and beginning of protraction) was 8 ms (Fig. 11, A and B) and was independent of the average protraction/retraction duration measured in each training condition. Thus the frequency of movement for the animals trained without cues was ~ 9 Hz (add protraction, retraction durations, and intervals between end of protraction and beginning of retraction), while the frequency of movement calculated for the animals trained with cues was ~ 11 Hz.

DISCUSSION

The main finding of this study is that adjacent whiskers often diverge in their movement; they move alone, move in different directions, and can even be retracted alone. Whiskers are therefore not constrained to move at the same time. These observations suggest that, in the whisker system, muscle synergies are dynamically modifiable (Bernstein 1967; Macpherson 1988). The results raise questions about the mechanisms underlying whisker movement.

Previous work on the whisker system has focused on the extraordinary anatomical organization and sensitivity of the tactile system (Carvell and Simons 1990; Guic-Robles et al. 1989; Hutson and Masterton 1986; Jenkinson and Glickstein 2000; Vincent 1912; Welker 1964; Woolsey and Van der Loos

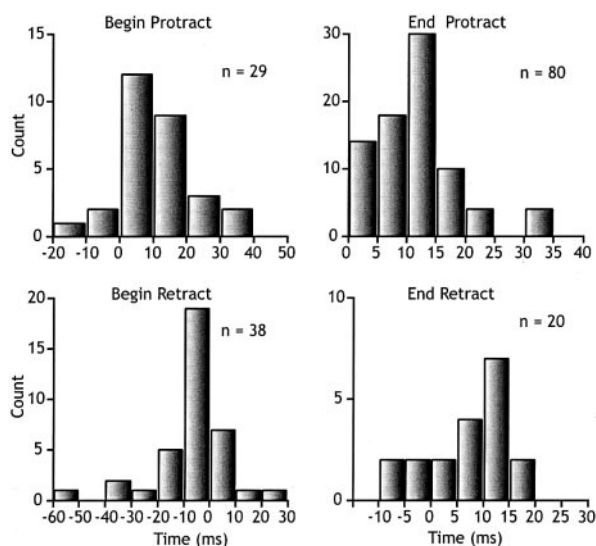
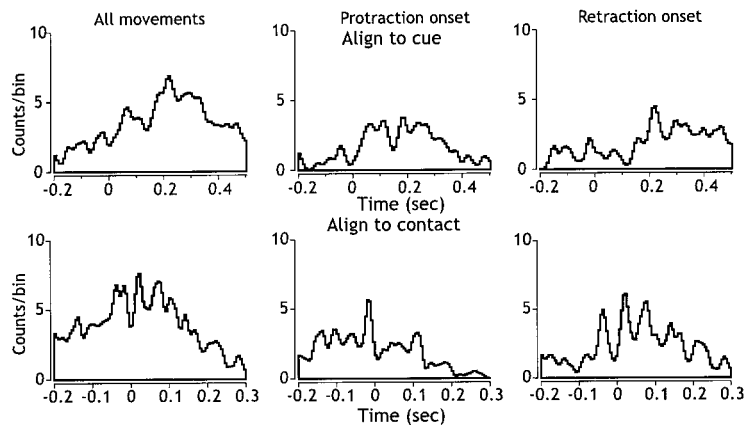


FIG. 7. Temporal differences between adjacent whiskers at the onset and end of movement. In some movements, there is a >4 -ms divergence in the onset and end times of movement of the adjacent whiskers. For constructing these histograms the movement onset time and movement end time for each whiskers were obtained. For those movements where a temporal difference was evident, the time difference is plotted. Note that the histogram for end of protraction includes 38 events where the rostral whisker made contact while the caudal whisker kept moving.

A Cue-Initiated



B Self-Initiated

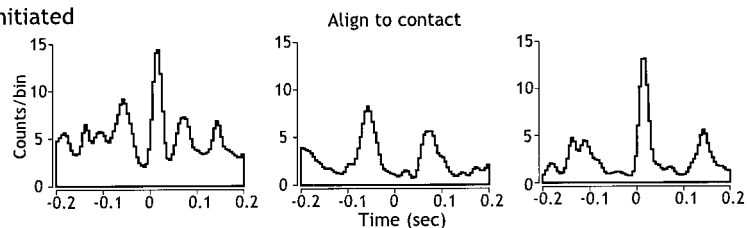


FIG. 8. Timing of whisker movement aligned to cue and contact in the cue-initiated (A) and self-initiated (B) movements. Whisker movement frequency increased after cue onset (top left) with protraction (top middle) increasing earlier than retraction (top right). Aligning the same movements to contact showed that whisker movement frequency increased around contact, with retraction frequency and protraction frequency increasing before contact. In the self-initiated contacts (B), the timing of both protraction and retraction are different from the timing of movement in the cue-initiated contact. See text for details. Bin size, 8 ms. Smoothing over 5 bins.

1970); the present study emphasizes the equally extraordinary motor system. The current generally accepted model of whisker movement is that single intrinsic muscles attached to each whisker (Dorfl 1982) move the whiskers in a single rostro-caudal plane around the head (Bermejo et al. 1996; Carvell and Simons 1990; Welker 1964). There are no known antagonists of the intrinsic muscles, and there are no complications of joints or muscle spindles (Dorfl 1982). Muscle synergies in this system consist of the intrinsic muscles moving each whisker and the extrinsic muscles moving the whisker pad en masse (Dorfl 1982, 1985; Wineski 1983). The oscillatory discharge of a brain-stem central pattern generator controls the whisking frequency (see Kleinfeld et al. 1999 for a review), which can be modulated by central control over the whiskers (Carvell and Simons 1991, and this study). Thus this system has several advantages over most other motor systems, the most important one being that each whisker's movement is indicative of the contraction or relaxation of a single muscle (Dorfl 1982). A second important simplification in this system is that the muscle spindle and golgi tendon organ activity has no role in

proprioception, movement, or in synchronization of motor units (Kirkwood et al. 1982; Sears and Stagg 1976; see Gandieva and Burke 1994 for a review).

Despite some evidence to the contrary, earlier studies have been content to describe whisker movement as synchronous. In the golden hamster, the orientation and position of whiskers (and consequently the distance between whiskers) changes as the animal moves (Wineski 1983). Wineski interprets these results as state changes; at rest the area covered by whiskers is less than when the animal is alert and whiskers are spread into a fan. During protraction whiskers are spread apart even further. In the present study, alertness plays no role. The distance between whiskers changes within single movements, as one whisker is protracted independently of another, or whiskers move in opposite directions. A study by Carvell and Simons (1990) also demonstrates divergent movement of whiskers. Small rostral whiskers and large caudal whiskers could be moved independently; rostral whiskers maintained contact, while caudal whiskers were swept back and forth over the discriminandum. This was taken as evidence that the caudal

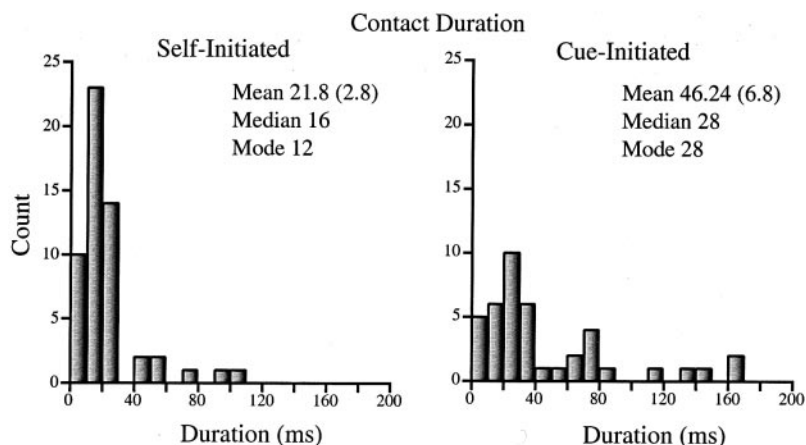


FIG. 9. Histogram of contact duration. Contact duration was significantly shorter ($P < 0.01$, Mann-Whitney U test) in the self-initiated (left) than the cue-initiated contacts (right).

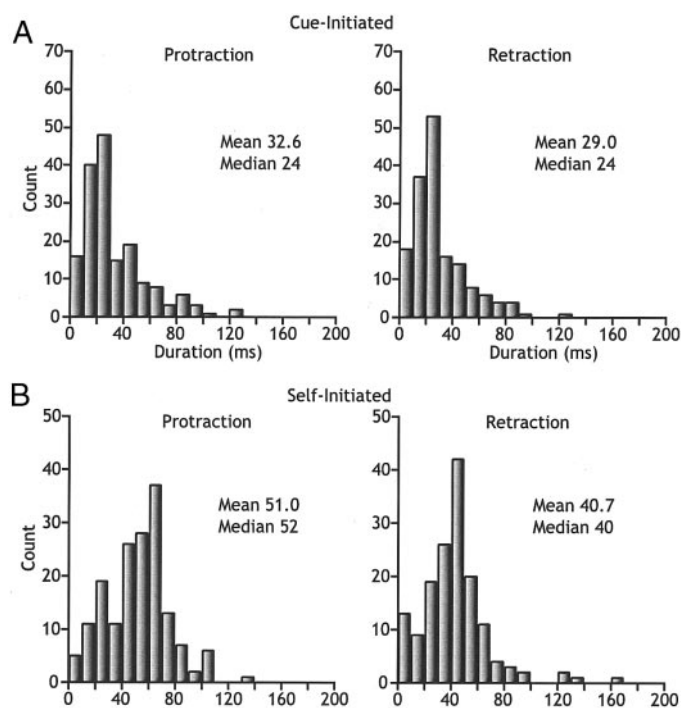


FIG. 10. Bar graph of protraction and retraction duration. The cue-initiated duration of movement are significantly ($P < 0.001$, Mann-Whitney U test) shorter than the self-initiated movement duration.

whiskers are used for discrimination of surface features. Clearly, the ability to move caudal whiskers independently of the rostral whiskers gives rats greater flexibility in performing roughness discrimination tasks (Carvell and Simons 1990). The present study shows that rats can even exert divergent control over individual caudal whiskers. The implication of independent retraction of whiskers is that the muscles (and motoneurons) controlling each whisker can be differentially activated and inactivated and that the muscle synergies are dynamically modified (Macpherson 1988). The attachment of whiskers and intrinsic muscles within the boundaries of the whisker pad places some limits on the extent of such independent movements but does not rule them out (Dorfl 1982). The retraction of individual whiskers also suggests that while retraction of whiskers may be passive, it need not be synchronous. The results are surprising enough that alternatives to independent control of whisker movement and some of the potential pitfalls associated with the methods are spelled out below.

An alternative explanation for the independent whisker movement is that there is a temporal phase lag or phase lead relationship between the movement of rostral and caudal whiskers. Phase differences could explain whisker movements in two different directions—the rostral whisker begins protraction even as the caudal is retracting—and the differences in timing of protraction and retraction of the adjacent whiskers. However, the phase model of whisker movement implies a strict timing difference on all movements, and the majority of movements of adjacent whiskers are synchronous within the 4-ms temporal resolution of this study.

The present study differs in many details from previous studies of whisker movement. Whiskers are trimmed to follow identifiable whiskers from day to day and trial to trial. Whis-

kers are also trimmed to control the whiskers used in the task. The whisking frequency reported in this study (9–11 Hz) falls in the range (0–20 Hz) reported in earlier studies (Bermejo et al. 1996; Carvell and Simons 1990; Fee et al. 1997; Gao et al. 2001; Welker 1964), suggesting that trimming whiskers does not substantially alter the pattern of whisker movement (also see Bermejo et al. 1996). However, it would be surprising if whisker trimming had no effect in how caudal whiskers are used (moved) (Krupa et al. 2001). In animals with a full complement of their whiskers, the caudal whiskers would rarely make contact and, if they did, would make contact for a very short duration because in tasks like the ones used in this study, the smaller rostral whiskers would make contact first (Sachdev et al. 2001). Thus in the intact animal, the dynamics of whisker movement are expected to be different and more complicated.

A second important methodological feature of this work is that the head is restrained. The head restraint probably alters some features of whisker movement, especially those features that relate to head movement, head orientation, or nasal contact (Welker 1964). However, it is precisely to control for head movement and to force the movement of only the whiskers that the head is restrained. Earlier work (Bermejo et al. 1996) and the present study suggest that parameters of movement, such as frequency of whisking are not altered by head fixation.

One of the other conclusions drawn from this work is that whisker movement lasts for surprisingly short times (usually between 12 and 80 ms). Although the frequency of whisking and the distance moved by whiskers have been reported earlier (Bermejo and Zeigler 2000; Bermejo et al. 1996; Carvell and Simons 1990, 1996; Fee et al. 1997; Gao et al. 2001; Welker 1964; Wineski 1983), the duration of protraction, retraction, and the interval between these movements have not. In this study the whisking frequency was 9–11 Hz, numbers similar to those obtained in all previous studies. Including contact dura-

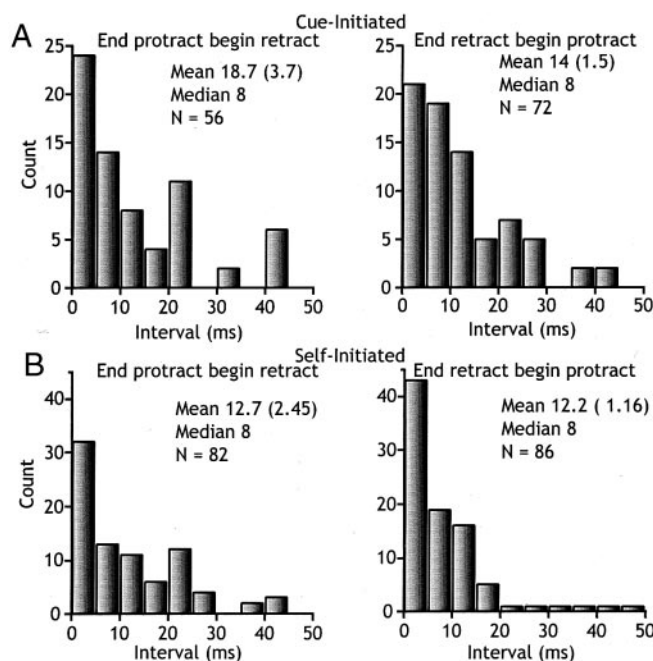


FIG. 11. Bar graphs of interval between movement. The median interval between the movements was not statistically different in the self-initiated and cue-initiated trials.

tion has a negligible effect on frequency of movement, suggesting that contact by itself need not substantially perturb the frequency of movement. Previous studies have described whisking as a protraction and retraction (Welker 1964; Wineski 1983). The movement of whisking is just protraction and retraction, but there is a measurable delay between protraction and retraction that contributes to all measurements of frequency. Each time whiskers stop for 8–12 ms, independent of whether the movement is a protraction or a retraction (Fig. 11). The delay between protraction and retraction could represent the relaxation/activation constant for muscles following cessation/onset of motoneuron discharge (Granit 1970). Actual recordings from the intrinsic muscles of single whiskers or from motor units associated with each muscle that could directly examine this question have yet to be successfully accomplished.

The brain stem mechanisms that control the movement and are responsible for the proprioception of whisker position also remain to be elucidated. A stretch reflex [stretch of the skin (the whisker pad), bending of single whiskers] for monitoring whisker position within the whisker pad and synchronizing movement of adjacent whiskers is one possibility (Fee et al. 1997; also see Gandieva and Burke 1994 for a review of function of cutaneous receptors in proprioception). Receptors associated with the deep and superficial vibrissal trigeminal nerve could contribute to this function (Dorfl 1985; Ranehan and Munger 1986; Rice et al. 1986; Waite and Jacquin 1992). Excitatory and inhibitory interactions between and within brain stem trigeminal neurons and facial nucleus motoneurons (Erzumulu and Killackey 1979; Kleinfeld et al. 1999) could also contribute. Stretch of extrinsic muscles is another possibility.

The use of whiskers in a contact task is remarkably precise and well controlled. Not only does contact stop the rostral whisker from moving, but contact rapidly stops the movement of the caudal whisker. This rapid end of caudal whisker movement could result from purely mechanical factors. The rapid stop could also result from contact-related feedback from the rostral whisker to motoneurons that control the movement of the caudal whisker. Efference copy or cortical corollary discharge controlling the movement of each whisker is another possible mechanism for stopping whiskers at the contact point (Evarts 1971; Nicolelis et al. 1995).

Finally, although the current model for whisker movement gives an exclusive role in whisker movement to the intrinsic muscles, the evidence for this model is purely anatomical (Dorfl 1982, 1985), not behavioral or physiological. An alternate model for protraction, retraction, and expansion and contraction of the whisker pad is necessary. It might be that for some whisker movements, specifically those made into the air or over a platform, the extrinsic muscles (those muscles that move the entire whisker pad) and intrinsic muscles work in a coordinated fashion (Berg and Kleinfeld 2001). For other movements or in particular behavioral contexts, the intrinsic muscles alone could be used for movement of the whiskers. Future work will examine these questions.

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