A multi-channel whisker stimulator for producing spatiotemporally complex tactile stimuli

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Abstract

A system is described that delivers complex, biologically realistic, tactile stimuli to the rat’s facial whisker pad by independently stimulating up to 16 individual facial whiskers in a flexible yet highly controlled and repeatable manner. The system is technically simple and inexpensive to construct. The system consists of an array of 16 miniature-solenoid driven actuators that are attached to 16 individual facial whiskers via very small (130 μm dia.) Teflon-coated stainless steel wires. When individual solenoids are energized, the wire is rapidly retracted, resulting in a deflection of individual whiskers. The rise time of deflection is approx. 1 mm/ms. Repeatable stimulation of individual whiskers can be achieved without touching adjacent whiskers, thereby allowing a very high density of stimulators to be attached within the spatially restricted region of the facial whisker pad. Complex patterns of whisker stimulation (designed to mimic biologically realistic stimuli) are delivered to the whisker pad by activating individual solenoid actuators in precisely controlled temporal patterns. These stimulations can be combined with multi-electrode single-unit ensemble recordings at multiple sites within the rat trigeminal somatosensory system. Analysis of neuronal population responses to these complex stimuli is intended to examine how the trigeminal somatosensory system encodes and processes spatiotemporally complex stimuli. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The rat facial whisker/trigeminal somatosensory system is widely used as a model system for studying the underlying neuronal properties and mechanisms that mediate encoding and processing of tactile stimuli in the mammalian brain. Among the many advantages of using this model system for somatosensory studies is the highly conserved spatial pattern of approx. 25 large facial whiskers (Brecht et al., 1997). In order to stimulate these whiskers during experiments, a mechanical stimulator is typically attached to an individual whisker and slightly deflected, causing a controlled stimulation of the particular whisker (see, for instance: Waite, 1973; Simons, 1983; Nicolelis and Chapin, 1994; Krupa et al., 1999). In some studies, two or three whiskers have been stimulated, either together or in close temporal sequences (see, for instance: Simons, 1985; Ghazanfar and Nicolelis, 1997; Goldreich et al., 1998; Shimegi et al., 1999). Generally, whiskers are stimulated multiple times while recording neuronal responses or activity to each stimulus. However, because of the relatively high spatial density of these facial whiskers, stimulating more than one or a small number of whiskers becomes difficult without inadvertently stimulating nearby whiskers.

The ability to stimulate large numbers of these facial whiskers in precise temporal and spatial patterns, however, is desirable for several reasons. For instance, such stimuli could simulate behaviorally meaningful stimuli a rat might normally encounter while exploring or navigating through its environment; an important factor for studies examining the complex neuronal and system level interactions that might mediate processing of biologically realistic tactile stimuli. Further, a system that can stimulate a large number of individual
whiskers would be extremely beneficial for studies that examine the neuronal response properties to stimulation of many different subsets of the large facial whiskers, for instance stimulation of individual rows or columns of whiskers (Ghazanfar and Nicolelis, 1997). Another use for a multiple whisker stimulator would be for plasticity studies where different combinations of whiskers are repetitively stimulated many times. Thus, a system that could stimulate many different whiskers without removing and repositioning a mechanical stimulator for each whisker would allow an experimenter to map receptive field (RF) properties of many sensory neurons, then perform a manipulation to the system (i.e. perform a peripheral nerve block or infuse a pharmacological agent) and then stimulate the same whiskers again without possible stimulus variations resulting from slightly different stimulator positions. Finally, such a system might be combined with a restrained rat to produce controlled, repetitive conditioned stimuli used in a behavioral learning context.

Here, we describe a simple system that is capable of stimulating any number of up to 16 facial whiskers in a highly controlled, repeatable yet very flexible manner. The system is not limited to stimulating 16 whiskers; more individual whisker stimulators could easily be added if desired. Further, this system is not limited to use in rats. The system could be modified to produce complex patterns of stimuli in a wide range of species including mice. This device consists of an array of miniature-solenoid actuators attached to individual whiskers via fine stainless steel wire. This combination allows a very high density of stimulators to be quickly yet accurately positioned within the spatially restricted region of the rat facial whisker pad. We used this system to deliver complex patterns of stimuli to the rat facial whisker pad while simultaneously recording single-unit ensemble activity within the ventral posterior-medial nucleus of the thalamus (VPM) and the barrel region of the primary somatosensory (SI) cortex (Krupa et al., 1998).

2. Methods

Our device consists of 16 individual stimulators that can be actuated independently in any desired spatial or temporal pattern. As stated above, the system is not limited to 16 stimulators. More channels could be added if desired. Each stimulator consists of three main components: (1) a miniature solenoid; (2) a very fine Teflon-coated, multi-stranded stainless steel wire within an outer Teflon guide tube; (3) controlling electronics (Fig. 1 and Fig. 2). Briefly, the system works as follows: One end of each of the fine stainless steel wires is fixed to the plunger of an individual miniature solenoid. Each wire passes through an individual Teflon guide tube that is approx. 45 cm long. The other end of each of the fine wires is formed into a small hook. By positioning the ends of the Teflon guide tubes just above the whisker pad of a head-restrained rat, the hooked end of the wires can then be attached to each of up to 16 individual whiskers without contacting neighboring whiskers. Individual whiskers are then stimulated by briefly energizing individual solenoids. Energizing a solenoid results in rapid retraction of the plunger that, in turn, retracts the fine wire within the Teflon tube. This retraction causes the attached whisker to be deflected in a controlled manner. De-energizing the solenoid causes the plunger to return to the original position which pushes the fine wire back to its original position, thereby returning the whisker to the initial resting position. This system functions in much the same way as a typical bicycle hand-brake cable system.

2.1. Mechanical assemblies

The first main component of this system, the miniature solenoid, produces the actual mechanical stimulus. The particular solenoids used in our system are Bicron model SCN0929-001 (Bicron Electronics, Canaan, CT, www.solenoid.com). These are 6 V, miniature, pull type solenoids. However, any similar miniature solenoid should work. Key criteria in choosing a particular solenoid design include: (1) low mass plungers; (2) approx. 2 mm of plunger travel; (3) sufficient pull force to retract the wire within the Teflon tube; (4) relatively compact size. Low plunger mass is important so that inertia is minimized. Minimal inertia is critical for fast stimulus rise and fall times. Sufficient plunger travel (or stroke) is necessary to achieve reliable whisker movement. The Bicron solenoids used in our system have a maximum pull force of about 12 oz. that is sufficient to move the fine wire in the Teflon tube.

The second main component of the system is the fine, Teflon-coated, multi-stranded, stainless steel wire within the Teflon guide tube (Fig. 3 and Fig. 4). This part of the system physically couples the plunger of the miniature solenoids to individual whiskers. The fine wire is a three-stranded, stainless steel Teflon-coated
Fig. 2. (A) Sixteen stimulators, arranged in four groups of four stimulators, attached to 16 individual whiskers. Note the 18 ga. stainless steel tubes clamped in place above the whisker pad by the polycarbonate holder as well as the 27 ga. tubes which guide the fine stainless steel wire through the whisker pad to an individual whisker which rests within the hooked end of the wire. (B) Layout of the individual solenoids and their associated driving electronics. In this case, 2 groups of 8 solenoids and drivers are positioned one above the other.
wire (wire diameter: 51µm; overall diameter: 130 µm, AM Systems # 7934). This multistranded wire is flexible enough so that the wire easily slides within the Teflon guide tube. The outer Teflon guide tube is 30 ga. tubing (0.3 mm i.d., 0.76 mm o.d., Small Parts, Inc. # HTX-27TW) and an 18 ga. stainless steel tube (18 ga.; 1.27 mm o.d.; 0.84 mm i.d.; Small Parts, Inc., # HTX-18) are cut to 4 cm lengths. The 30 ga. Teflon tubing is cut into 45 cm lengths. One end of each of the Teflon tubes is flared slightly so that one of the 27 ga. stainless steel tubes can be pressed into the end. A 27 ga. tube is then pressed approx. 1 cm. into the flared end of a Teflon tube. A drop of cyanoacrylate adhesive (superglue) is placed at the flared end of the Teflon tube, allowing some of the glue to flow up into the flared end. This glue bonds the 27 ga. stainless steel tube to the Teflon guide tube. Before the glue dries, a 4 cm length of 18 ga. tube is then slid down to the end of the Teflon tube and pressed over the outer flared end. This pinches the Teflon tube tightly around the 27 ga. tube and tightly within the 18 ga. tube thereby locking all three tubes together.

The purpose of this assembly is two-fold. The outer, 18 ga. tube is clamped in a holder just above the rats' whisker pad thereby positioning the 27 ga. tube and fine wire just above an individual whisker (Fig. 2). The inner, 27 ga. tube acts as a guide through the whisker pad for the fine wire. Because the diameter of this tube is very small, it can be positioned in between several whiskers without touching them, thereby allowing the hooked end of the fine wire to be attached to a single whisker. This ability to position the 27 ga. guide tubes within the whisker pad without touching neighboring whiskers is critical for attaching 16 stimulators to 16 whiskers.

Fig. 2 and Fig. 3 show two different methods of holding the whiskers with the fine Teflon-coated stainless steel wire. Fig. 2 shows a V-shaped hook at the end of the wire, while Fig. 3 shows a loop shaped hook at the end. The V-shaped hook is more useful when it is desirable to allow the whisker to return to its rest position at its own rate after a stimulus. The loop shaped hook (Fig. 3) holds the whisker more securely. But, with this design, the whisker is returned to its rest position at the same rate as the solenoid plunger. Both means of attaching whiskers to the fine wires have been used with equal ease and success. The flexibility of this system allows other designs to easily be implemented if certain experimental conditions required a new design.

The other end of the Teflon guide tube, the end that guides the fine wire into the solenoid plunger, is constructed exactly as above with the following exception: the length of the 18 ga. and 27 ga. tubes is only 2 cm (Fig. 2B and Fig. 4). The 18 ga. tubes are used to clamp the guide tubes in front of and in line with the solenoid plungers (Fig. 2B). The 27 ga. tube aligns the fine wire with the center of the solenoid plunger.

The fine stainless steel wire is physically attached to the plunger of a solenoid as follows (Fig. 4). A small hole is drilled down the center of the plunger, approx. 5 mm deep. A 21 ga. stainless steel tube is glued into
this hole using cyanoacrylate. This 21 ga. tube has a small slot cut about half way through, about 1 mm from the end (see inset, Fig. 4). The fine wire passes out of the 27 ga. tube and into the center of the 21 ga. tube. The wire is then passed out through the small slot. A short length of polyethylene tube (0.76 mm i.d.; 1.22 mm o.d.; approx. 1.5 cm length) is then pressed over the end of the 21 ga. tube. This locks the fine wire to the end of the 21 ga. tube by pinching it between the polyethylene tube and the outside of the 21 ga. tube (inset, Fig. 4). The polyethylene tube also fits over the 27 ga. tube. In addition to locking the fine wire to the 21 ga. tube, the polyethylene tube also prevents the fine wire from bending or kinking when the solenoid is de-energized and pushing the fine wire back into the Teflon guide tube to return a stimulated whisker to rest position. This attachment assembly provides a very reliable means of attaching the fine wire to the solenoid plunger. In addition, it also allows the fine wire to be replaced easily and very rapidly if it should become damaged.

The holder that positions each of the individual Teflon guide tubes above the rat’s whiskers is shown in Fig. 2A. In this particular case, four groups of four guide tubes are clamped together and positioned above one side of the rat’s face. The individual clamps are simply two strips of polycarbonate held together by a screw at both ends of the strips. Sandwiched between the two strips is a thin strip of foam rubber. The 18 ga. stainless steel tubes are clamped between the polycarbonate strips; the foam rubber provides some grip on the 18 ga. tubes. The important design characteristic of this clamping system is that although the 18 ga. tubes are held firmly between the polycarbonate strips by the foam rubber, individual tubes are still able to be manually angled or moved up or down within a clamp. This allows the hooked end of each individual fine wire to be positioned precisely above a desired whisker and attached to that whisker and then left in that position. For example, at the beginning of each experiment, all of the individual 18 ga. tubes are pulled up within the clamps. Then, once the rat’s head has been fixed in place, individual guide tubes are gently lowered and angled toward target whiskers. The individual 27 ga. portions of the guide tubes are thus ‘threaded’ down in between neighboring whiskers without touching them until all 16 stimulators have been attached to individual whiskers without touching any neighboring whiskers. This entire procedure proceeds quite rapidly, typically taking less than 10 min. Because the guide tubes are held firmly within these clamps, no inadvertent extraneous vibrations or movements are passed to the whiskers during an experiment.

Each of the individual clamps is mounted above the rat’s face by attaching the clamp to another larger piece of polycarbonate that is fixed upright in front of the rat. However, any number of mounting schemes are possible. For instance, in some experiments, we have attached eight stimulators to each side of a rat’s face to produce bilateral stimuli. In other experiments we attached eight stimulators directly above eight whiskers to produce a dorsal-ventral stimulation and eight stimulators directly in front of those whiskers to produce a rostral-caudal stimulation thereby creating directionally variable stimuli. It would also be quite easy to mount these clamps to stereo-platforms thereby allowing stimulation of whiskers in a rat that is mounted in the stereotax. Because each individual guide tube stimulator is completely independent, tremendous flexibility in the arrangement of stimulators is possible.

The solenoid ends of the guide tubes are clamped down in a similar fashion as above (Fig. 2B). As shown in Fig. 2, eight solenoids are mounted on a sheet of polycarbonate and eight guide tubes are aligned with the center of the plunger axis and clamped in place. Eight additional channels are mounted below. Also shown are the associated solenoid driver electronics.

Individual solenoids are mounted to the sheet of polycarbonate as follows (Fig. 2B and Fig. 4). The individual solenoids are first attached to a ‘U’ shaped solenoid mounting bracket (Fig. 4). A small slot is cut in the tail end of this mounting bracket and the bracket is affixed to the polycarbonate sheet with a mounting screw positioned in the slot.

This solenoid mounting system also provides a means for adjusting the amplitude of the whisker stimulation. Loosening the mounting screw allows the solenoid to be moved forward or backward relative to the end of the Teflon guide tube. Typically, the solenoid is moved forward until the end of the polyethylene tube contacts the end of the Teflon guide tube (Fig. 4A). The solenoid is then pushed forward a bit more, thereby partially compressing the spring and pushing the plunger in. The solenoid is then locked into position. When the solenoid is energized, the plunger is retracted all the way into the solenoid. When the solenoid is then de-energized, the compressed spring pushes the plunger back to the original position with the polyethylene tube against the end of the guide tube. In short, the amplitude of stimulation is set as the distance between these two mechanical stop points. Thus, by simply repositioning the solenoids relative to the ends of the guide tubes, stimulus amplitudes can be precisely set and maintained. Further, it would be fairly simple to modify this solenoid positioning scheme so that individual solenoids can be moved via remote control, for instance, using a small stepper motor. With such a system, stimulus amplitude could be continuously varied from stimulus to stimulus.
2.2. Solenoid control and driving electronics

The circuit used to drive individual solenoids is shown in Fig. 5. This simple circuit consists of a TTL compatible line driver (7407) that switches a power transistor (SK3180). The solenoid control signal is a TTL compatible pulse. When this signal goes high, the power transistor conducts causing the solenoid to be energized. Energizing the solenoid causes the plunger to retract which results in deflection of the attached whisker. When the control signal goes low, the solenoid is de-energized which returns the plunger (and the attached whisker) to the original rest position. Thus, the duration of a whisker deflection is controlled by the pulse duration. Of course, any circuit of similar design should work fine.

Different patterns of whisker stimulation are achieved by energizing different solenoids at precisely controlled intervals. Generating these control patterns can be achieved in any number of ways ranging from simply hard wiring TTL compatible circuit elements that generate fixed patterns to sophisticated computer controlled programs that output any desired pattern via a TTL compatible computer interface. We have used two different computer programs to generate stimulus patterns.

For instance, one system uses the Tempo (Reflective Computing, Inc., St Louis, MO) computer programming language to generate different patterns of stimuli. This DOS/Windows compatible program outputs control pulses to the solenoid controller electronics via a ComputerBoards DAS1602/12 input/output card (ComputerBoards, Inc., Mansfield, MA) in a standard, IBM compatible computer. This particular system has a total of 24 TTL compatible digital outputs. With this system, 16 channels are used to control each of the 16 individual stimulators and the remaining eight channels are used to interface with a multi-channel neural acquisition processor (MNAP, Plexon, Inc., Dallas TX) that is used to simultaneously record from up to 48 microwire electrodes. These eight interface channels are used to send an 8 bit binary word to the MNAP. This 8 bit interface serves two functions. First, interface signals sent to the MNAP allow precise synchronization between recorded neuronal spike trains and onset of whisker stimuli. Second, the 8 bit binary word encodes different stimuli patterns and this code is stored with the recorded neural spike data. With this system, up to 128 different patterns of whisker stimuli can be presented to the rat and stored with the recorded neural data which facilitates accurate, precise and efficient analysis of recorded neuronal activity.

An example of five different stimuli patterns delivered in one experiment are shown in Fig. 6. In each of these patterns, different whiskers are stimulated in a precise temporal pattern to simulate a stimulus ‘wave’ rapidly sweeping across the whisker pad. Each of the five different patterns differs very slightly in the exact whiskers stimulated. These patterns of stimuli were delivered while ensemble neuronal activity was simultaneously recorded from populations of single neurons in both the SI cortex and the VPM thalamus.

2.3. Measuring stimulator rise and fall times

We measured the actual movement of the stimulators to ensure that they accurately followed the control signal and to ensure that there were no unwanted mechanical oscillations in the system when stimulators were energized and de-energized. To measure stimulator movement, the hooked end of individual stimulator fine wires was attached to one end of a thin film Piezo element (AMP, DT1-028K). The other end of the Piezo film was fixed in a mount. These Piezo films are very thin (200 μm), very flexible films that produce a voltage when flexed. This voltage is proportional to the degree (or amplitude) of flexation with a high degree of accuracy. Thus, as the stimulators are energized and the fine wire is retracted, the film is flexed producing a voltage that is proportional to the amplitude of movement. When the stimulators are de-energized, the film is returned to the initial position which returns the Piezo signal voltage to 0 V. The output signal from this Piezo film detector was amplified (10 × ) and displayed on a digital oscilloscope that could capture and save test stimuli. Also displayed on the oscilloscope were the stimulator control signals. These output signals were then compared to ensure the accuracy and repeatability of stimulator deflections (Fig. 7).

2.4. Ensemble neuronal recordings in VPM and SI cortex

Single unit ensemble neuronal activity was recorded from populations of neurons in the VPM thalamus and the SI cortex of pentobarbital anesthetized rats while facial whiskers were stimulated either individually or in
Fig. 6. Example of 5 different complex stimulus patterns. Each grid of 16 points represents the 16 individual stimulators attached to 16 individual whiskers (rows B, C, D, & E and columns 1–4). A large black circle within the grid represents an activated stimulator. Thus, in the top row of 7 grids (row 0), 1 whisker (E1) was stimulated for 5 ms (shown in the leftmost grid) starting at time 0 ms. Fifteen milliseconds later, whiskers D1 and E2 were simultaneously stimulated for 5 ms (second grid). Fifteen milliseconds later (40 ms after the onset of the first stimulus), whiskers C1, D2, and E3 were simultaneously stimulated for 5 ms (third grid). The fourth grid shows whiskers B1, C2, D3, and E4 stimulated. The pattern continues for three more grids until whisker B4 alone is stimulated. This pattern of stimuli creates a stimulus ‘wave’ that simulates an object sweeping across the whisker pad from the ventral posterior corner upwards to the dorsal anterior corner at a rate equivalent to the normal whisking frequency of about 8 Hz. In each of the lower rows (1–4) the original pattern is repeated except that one or more whiskers originally stimulated in pattern 0 are not stimulated. These non-stimulated whiskers are represented as open circles.

complex spatial or temporal patterns. The details of the electrophysiological recording procedures are described in great detail elsewhere (Nicolelis and Chapin, 1994; Nicolelis et al., 1997). Briefly, arrays of 16 Teflon-coated stainless steel microwire electrodes were stereotaxically implanted in the left VPM thalamic nucleus and in the barrel region of the left SI cortex in female Long–Evans rats (approx. 250 g). Following 7 days of post-surgical recovery, rats were lightly anesthetized (pentobarbital) and placed in a head holding device (Fig. 2A). Individual stimulators were attached to 16 facial whiskers as described above. Stimulators were attached to the following whiskers: B1–4, C1–4, D1–4 and E1–4. Single unit neuronal activity was isolated on the individual microwire electrodes as described elsewhere. Once unit activity was isolated, each of the individual whiskers as well as groups of up to 16 whiskers were stimulated. An example of different patterns of whisker stimulation are show in Fig. 6. Each whisker was stimulated individually a total of 150 times and each pattern was also presented 150 times. Stimuli were presented in a random fashion at a rate of 1 Hz.

Fig. 7. Movement of a typical stimulator transduced from the output of a thin piezo film movement detector. Note the very fast stimulus rise time and near absence of mechanical ringing even though the control signal is a step function.
3. Results

3.1. Stimulator rise and fall time

The rise and fall times of a typical stimulator are shown in Fig. 7. The velocity of stimulator deflection is about 1 mm/ms. This was very repeatable from stimulus to stimulus and was also very similar between different individual stimulators. There was very little oscillation of the stimulator at the end of either the rising or falling phase of the stimulus. This results from both the damping effects of the fine wire sliding within the Teflon tube and the fact that the fine wire is pulled in the same linear direction as the solenoid plunger.

There was a very slight delay between the onset of the stimulus command signal and the actual movement onset of the stimulator (approx. 1.2 ms, Fig. 7). Further, the stimulus did not reach maximal amplitude until approx. 2 ms after the command onset. These very small delays are likely a result of overcoming initial inertia of the solenoid plunger and fine wire. Again, these delays were very repeatable from stimulus to stimulus. Because of these delays, minimal stimulus duration for this system was about 3 ms. Typically, stimuli with durations of 5 ms were reliably and repeatably delivered as part of a complex stimulus pattern (i.e. Fig. 6). Note, the minimal stimulus duration of 3 ms compares quite favorably with stimulus durations of 10 to 100 s of ms that are commonly used in whisker related experiments (Nicolelis and Chapin, 1994; Peterson et al., 1998; Simons, 1985; Waite, 1973). Further, the characteristics of this system, for instance very fast stimulus rise time and minimal mechanical oscillation, are as good as or better than other systems commonly employed to stimulate facial whiskers (Corey and Hudspeth, 1980; Peterson et al., 1998; Simons, 1983; Stephen, 1969; Waite, 1973).

3.2. Neuronal response patterns

Neural activity of populations of single neurons located in the VPM and barrel region of the SI cortex was recorded while individual whiskers and complex patterns of many whiskers were stimulated. Examples of neuronal responses are shown in Fig. 8. Stimulation of individual whiskers resulted in highly significant, short latency responses in VPM neurons (Fig. 8A, left two columns). Responses of SI cortical neurons were similar to VPM responses but the onset latencies were slightly longer (Fig. 8A, right two columns). These response patterns were very similar to responses of VPM and SI neurons reported previously that were elicited by stimulating whiskers by other means (Nicolelis and Chapin, 1994; Ghazanfar and Nicolelis, 1997; Krupa et al., 1999). Further, the responses of individual neurons were very repeatable demonstrating the repeatable nature of the stimuli. In Fig. 8A, the upper histograms in each of the four columns represent the response of an individual neuron to stimulation of an individual whisker. The lower histograms represent the responses of the same neurons to stimulation of the same whiskers 3 h later.

Fig. 8B shows the response of a population of 20 VPM neurons to stimulation of an individual whisker (D2, left panel) and a patterned stimulation of 16 whiskers (right panel). In this example, the patterned stimulation was designed to simulate a stimulus sweeping across the whisker pad. As expected, the population response to the complex patterned stimulus (right panel) is substantially different from the response to the single whisker stimulus (left panel). The responses of neurons to the patterned stimulus are much more prolonged compared with the single whisker stimulus. Several neurons that did not respond to the single whisker stimulus did respond to the patterned stimulus. Overall, response magnitudes were also greater with the patterned stimulus.

4. Discussion

Several different techniques for whisker stimulation have previously been described. Perhaps the simplest method is just manually stimulating individual whiskers with different probes while monitoring for responses through an audio feedback. While this system provides a very quick and easy means of subjectively evaluating whether a cell responds to stimulation of a particular whisker, the lack of stimulus control precludes any quantitative analysis of responses. A more precise method of whisker stimulation involves deflecting individual whiskers with a small electro-magnetic motor or galvanometer (Stephen, 1969; Waite, 1973; Ito et al., 1979; Nicolelis and Chapin, 1994; Shimegi et al., 1999). This technique allows precise control of stimulus onset and amplitude, thereby facilitating quantitative analysis of neuronal responses. However, this method is generally limited to stimulating only a single whisker or a very small number of whiskers at a time. Further, the stimulator must be accurately positioned onto each whisker stimulated, a time consuming procedure that can limit the number of whiskers stimulated during a given experiment. Another technique is to stimulate whiskers with small air currents (Hutson and Masterton, 1986). This technique can be useful in certain experimental procedures, such as with an awake, restrained rat. However, this technique lacks both the spatial and temporal precision of other stimulus techniques. Yet another technique that has been used in a number of studies involves the use of piezoelectric bimorphs (Corey and Hudspeth, 1980; Simons, 1983). This particular stimulus method has the advantage that
Fig. 8. (A) Peri-event histograms showing the responses of individual neurons to stimulation of individual whiskers. Neurons 2a and 4c were recorded in VPM and neurons 17a and 18b recorded in the SI cortex. In each case, the upper histogram shows the response to stimulating the whisker 150 times. The lower histogram shows the response resulting from stimulating the same whiskers at least 3 h later. Note the high degree of repeatability of responses. (B) Neuronal population responses (recorded in VPM) to stimulation of a single whisker (D2, left panel) and to a complex pattern stimulus representing a wave sweeping across the whisker pad. Each stimulus was presented 100 times (see Fig. 6 for description of the stimulus patterns, lower portion of 8B). The 3D surface plots represent the cumulative post-stimulus responses of 20 neurons.

The direction of whisker stimulation, as well as amplitude, can be continuously varied. This provides a simple means of evaluating the directional tuning properties of individual somatosensory neurons as well as responses to ‘noisy’ stimuli, i.e. stimuli that are not simple steps, ramps, or sinusoids. However, this system has only been used to stimulate single whiskers, or small subsets of whiskers. In order to stimulate larger number of whiskers, each piezoelectric stimulator must be removed and carefully repositioned onto different whiskers. Also, relatively high voltages (> 100 V) are frequently required to drive the piezoelectric bimorphs.

The multi-channel whisker stimulus system described in the present paper delivers tactile stimuli to the rat facial whiskers in a very reliable, very repeatable yet highly flexible manner. The system is capable of stimulating individual whiskers or any combination of up to 16 whiskers and can be easily expanded to include more whiskers. Complex patterns of stimuli, which vary either spatially or temporally, can be delivered to the whisker pad by varying the timing of individual whisker stimuli (Fig. 6). These patterns of stimuli can be used to examine, in a controlled and quantitative manner, the complex interactions among populations of somatosensory neurons in response to biologically realistic stimuli. Further, combining these stimuli with ensemble neuronal recordings at multiple levels within the trigeminal somatosensory system, provides a means to begin to examine how populations of somatosensory neurons might encode and process the multidimensional (i.e. spatial, temporal, directional) aspects of tactile stimuli that an animal might encounter during normal behavior.
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