

Active touch, exploratory movements, and sensory prediction

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Synopsis The relation between somatosensory input and motor output is asymmetric. Somatosensation is associated with every movement an animal makes, but movement is not required for somatosensation. This symposium paper proposes a classification scheme for movement, in which movements are placed along a continuum that describes the role that somatosensory information plays during the movement. Fine sensorimotor control—manipulation and exploration—are found to fall to one extreme of the spectrum, and exploratory movements in particular are shown to possess characteristics that clearly distinguish them from other varieties of movement. Specifically, the exploratory process must permit animals to extract an object's features independently of the sequence of movements executed to explore the object. Based in part on our work on the rat vibrissal system, we suggest that exploration of objects may consist of two complementary levels of sensorimotor prediction operating in parallel. At the cognitive level, the animal might move so as to perform *hypothesis testing* about the identity or nature of the object. The particular hypothesis tests chosen by the animal might be implemented through sequences of *control-level predictions* that could be generated at the level of the brainstem and cerebellum.

Introduction: the importance of biomechanics to the study of sensory systems

When we imagine how animals move, the first images that come to mind are of locomotion: animals leap, scurry, slither, fly, swim, and creep. Animals also make many movements, however, that have little to do with getting from point A to point B. Some of these nonlocomotor movements, such as withdrawal from a noxious stimulus, or grooming and scratching, are reflexive or patterned movements. Other movements, however, are used to explore the external environment and to manipulate objects, and these cannot be entirely reflexive or patterned, since they depend critically on context, memory, behavioral state, or desired outcome; in short, on what we might call “higher level” processing.

An animal's exploratory movements make preferential use of sensory modalities specialized for its ethological niche. Rats, as nocturnal, burrowing creatures, have poor visual acuity, but an excellent sense of smell, and their lips and whiskers (vibrissae) are acute tactile sensors. Humans, by contrast, have a relatively poor olfactory sense, but highly developed visual systems and sensitive tactile reception on the

fingertips. Even the most sensitive of sensory systems, however, cannot possibly apprehend the totality of data provided by the external environment. Animals must determine which portions of incoming data are relevant to the current behavioral task, and must select and refine their movements in ways that acquire the most salient sensory information.

Because sensory data are acquired through movement, biomechanical analysis is critical to the study of sensory systems. This analysis must span at least two levels of description. One level must include the mechanical constraints imposed by the physical instantiation of the sensor, including material properties (e.g., the viscoelastic properties of the skin), actuation mechanism(s), spatiotemporal limits on actuation and sensor response, and the passive dynamics of the motor plant. A second level must describe how the motor commands selected by the animal drive the sensor in question. The animal's choice, of which degrees of freedom to employ, will depend on the particular task being performed. In turn, these choices shape the animal's perceptions and thus, presumably, the animal's “cognition.” In the field of artificial intelligence, the idea that perception and cognition are at least partially determined by the body's mechanics is

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termed “embodiment,” but this basic idea has been a thread through the literature at least since Katz (1925, in Kruger 1989).

This symposium paper has two goals, both pertaining to the second level of description. First, we propose a scheme for the classification of movement, in which movements are placed on a spectrum based on the role of somatosensory information during the movement. Fine sensorimotor control—manipulation and exploration—are found to fall to one extreme of the spectrum, and exploratory movements, in particular, are shown to possess characteristics that clearly distinguish them from other varieties of movement.

Second, we examine the particular characteristics of exploratory movements that may permit animals to extract invariant features of an object, regardless of the exploratory sequence of movements performed. Based in part on our work on the rat vibrissal system, we suggest that exploration of objects may consist of two complementary levels of sensorimotor prediction operating in parallel. At the cognitive level, the animal might move so as to perform *hypothesis testing* about the identity or nature of the object. The particular hypothesis tests chosen by the animal might then be implemented through sequences of *control-level predictions* that could be generated at the level of the brainstem and cerebellum.

All possible states for a sensory surface and its associated muscles

What types of somatosensory information do animals use when moving? Somatosensation is traditionally divided into four major perceptual modalities: tactile, proprioceptive, thermal, and pain. Of these, tactile and proprioceptive sensations are particularly important for guiding movements. Tactile sensations are elicited by mechanical displacements of exteroceptors; these sensations are what we usually think of as “touch.” Proprioceptive sensations are usually internally generated, and consist of information about the mechanical variables associated with the muscles and joints. Through proprioceptive systems an animal gains information about the relative positions, velocities, and forces exerted by and on its limbs.

Figure 1 schematizes all possible muscle activation and movement states for any given sensory surface. The muscles controlling the surface can either be active or inactive, and the surface can either be immobile or moving. Muscles can be inactive only during a completely relaxed posture, when no muscle

	Sensory Surface Immobile	Sensory Surface Moving
Muscle Inactive	Relaxed Posture	Movement caused by external force(s)
Muscle Active	Postural Maintenance, Isometric Contractions	Movement caused by muscles controlling the sensory surface

Fig. 1 Possible states of muscle activation and movement for a sensory surface.

forces are acting in opposition to gravity. If the sensory surface is acted upon by a sufficiently large external force, it will be set in motion. These two conditions occupy the first row of Fig. 1.

Conditions of complete muscle inactivity are quite rare in normal animals, even when sensory surfaces are immobile. Normal postural maintenance requires muscle activation, as does tensing a muscle without moving a limb (isometric contraction). In the fourth remaining possible state for a sensory surface, muscles are active and the surface moves as a consequence. These are the conditions generally thought of as encompassing “motor control,” distinct from postural maintenance and passive limb displacements, and this category includes an enormous range of possible movements and somatosensory activity.

Passive somatosensation

The relation between somatosensory input and motor output is asymmetric. Excluding some disease states, somatosensation is necessarily associated with every movement an animal makes, but movement is not required for somatosensation. This asymmetry makes it possible to distinguish between two types of somatosensation, based on the degree of motor activity associated with the sensory input.

We suggest the term “passive somatosensation” to refer to sensory inputs generated independently of activation in the muscles controlling the sensory surface. We suggest the term “active somatosensation” to refer to sensory inputs resulting from activation in the muscles controlling, and/or movement of, the sensory surface.

Figure 2 schematizes the different types of passive somatosensation, superimposed on the categories of

	Sensory Surface Immobile	Sensory Surface Moving
Muscle Inactive	PASSIVE SOMATOSENSATION Proprioception	Proprioception
Muscle Active	Exteroception	Exteroception

Fig. 2 Passive somatosensation. Note that although passive exteroception can occur even when the muscle is active (e.g., an external object can touch you while you are moving), passive proprioception can occur only when the muscle is inactive.

muscle activation and movement shown in Fig. 1. Passive somatosensation includes both exteroceptive and proprioceptive sensations. Passive exteroceptive sensations are necessarily generated by an agent external to the sensory surface in question.

Passive somatosensation when a sensory surface is immobile is essentially synonymous with a sense of resting posture. During fixed, resting posture, static proprioceptive inputs provide an animal with a sense for where its limbs are in space and relative to each other. At the same time, static exteroceptive inputs allow the animal to sense external objects impinging on its body. For example, a person can easily feel the surface of the table her arm is resting on. Static exteroception and proprioception are closely intertwined, and it is thought that the same deep pressure receptors probably mediate both sensations (Edin 1992; Collins and Prochazka 1996).

Movement of a sensory surface whose associated muscles are completely inactive is rare but might occur when a doctor displaces a patient's limb to examine muscle tone, or during an unpleasantly limp handshake. In these instances the passive person experiences not only externally-generated exteroception, but also changes in proprioception independent of the signals in his limbs' motor neurons. Passive limb displacements are perhaps more frequently found under experimental conditions than in the course of everyday life. They are often used in psychophysical and physiological experiments to determine which part of a perception or of a neural response is generated by motor activity proper, and which by the activity of the associated proprioceptors.

Passive exteroception is necessarily generated by an agent external to the sensory surface. Because

active and passive somatosensation are defined with respect to a particular sensory surface, and not with respect to the animal as a whole, it is possible to have self-generated, passive exteroception. For example, when a person uses his right hand to scratch an itch on his (motionless) left, the sensations elicited in the left hand are static proprioception and passive, dynamic exteroception. The sensations elicited in the right hand, which is actively scratching, are quite different, and will be discussed in more detail later. Passive exteroceptive sensations can, of course, be generated by objects or beings other than the animal. These sensations arise when someone pats you on the back, when an apple falls on your head, or when a spider runs across your leg.

Which of the passive somatosensations discussed above would we call "touch"? Earlier it was suggested that touch could be defined as the mechanical displacement of exteroceptors. Following this definition, all of the exteroceptive experiences described above—the feel of the surface of a table your arm is resting on, an apple falling on your head, a spider running across your leg, scratching an itch—would be called forms of "passive touch." This description of passive touch is in fact the one used in the scientific literature, and implies that touch is a purely physiological phenomenon (the activation of exteroceptors). Our sense of passive touch is quite versatile: we can distinguish between stimuli that push, slap, pat, tap, prick, scratch, exert pressure, scrape, rub, slide, brush, roll, vibrate, stretch, knead, and pinch (Gibson 1962).

Active somatosensation

Like passive somatosensation, active somatosensation encompasses both proprioception and exteroception. Figure 3 diagrams the different types of active somatosensation, superimposed on the schematics of Figs. 1 and 2. Muscles controlling a sensory surface may be active even if the surface is immobile, as during normal postural maintenance or isometric muscle contractions. Under these conditions, somatosensation is entirely proprioceptive. No exteroceptive inputs are present, unless they are generated by an external agent, as during passive touch.

In contrast, conditions in which muscles actively control a moving surface generally result in both proprioceptive (kinesthetic) and exteroceptive sensations. As indicated by the examples within the diverging arrows of Fig. 3, these conditions include an enormous variety of movements, ranging from

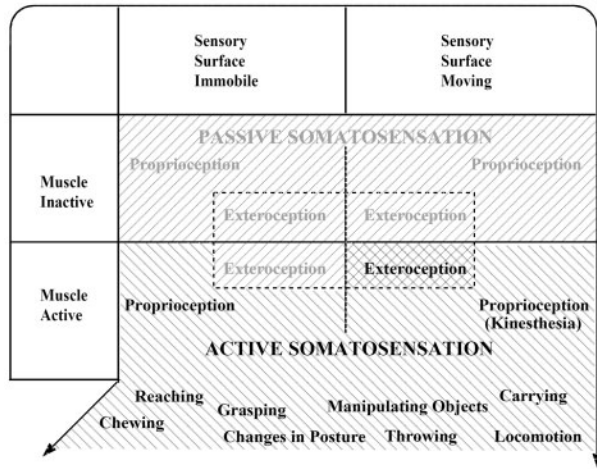


Fig. 3 Active somatosensation.

locomotion and postural changes, to manipulation and to us of tools.

By analogy to passive touch, and consistent with a purely physiological definition of “touch,” one might think that *all* exteroception during active somatosensation would be termed “active touch.” This does not turn out to be the case. Instead, our use of the word “touch,” both colloquially and scientifically, includes sensations arising only from movements *intended to elicit a sensation*. There are, however, many somatosensations that arise during “non-touching” movements—movements with the goal of *displacing* a limb or an external object. These movements might well stimulate the identical receptors as those stimulated during a “touching” movement. Yet we do not call these sensations “touch” colloquially, and they are not in fact included in the standard scientific definition of active touch. “Active touch” applies only to movements, in which a sensory percept or intent dominates. *The term active touch involves not only activation of receptors (a physiological variable) but also movement intent (a psychological variable).*

The intent behind a particular movement, however, is often difficult to ascertain. Indeed, most movements may be said to have both sensation and displacement as goals. For example, the action of hammering requires accurate sensation of the hammer’s properties (e.g., its mass and length, and the slipperiness of its handle) and also displacement of the limb and hammer. Because somatosensory and displacement goals are so often intertwined, movements are not easily divided into these two hard and fast categories. Instead, Figure 4 illustrates the different types of active somatosensation along a

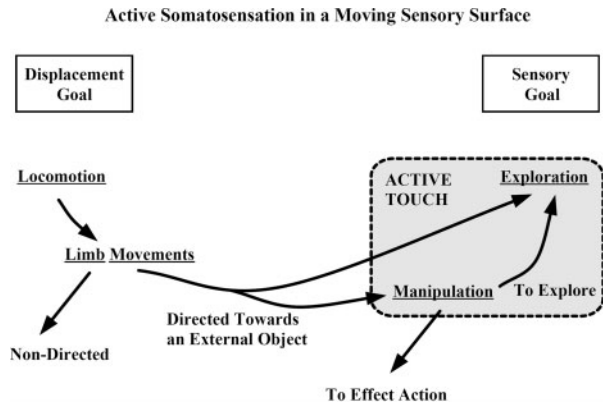


Fig. 4 The spectrum of active somatosensation.

spectrum, ranging from a dominant displacement goal to a dominant sensory goal.

Movements along the spectrum of active somatosensation

That locomotion falls far on the “movement goal” side of the spectrum of active somatosensation is revealed by the fact that it is rarely—if ever—called a form of somatosensation, despite its extensive use of sensory inputs. Locomotion requires that each limb be moved in a regular temporal and spatial relation to the others. Although this regularity requires significant interlimb coordination, it also means that locomotion is a more redundant computational problem than is the independent movement of single limbs or sets of limbs. During locomotion, the movement of one limb provides information about subsequent movements of the others. In contrast, when a limb moves independently, its kinematics might provide little if any information about the positions or movements of any other body part.

Examples of independent limb movements include shifting posture, stretching, reaching, pointing, hitting, and kicking. In mammals, the coordination necessary for independent movements of limbs relies heavily on the corticospinal tract, which directly connects the neocortex with the spinal cord. Comparative studies across mammals suggest that the extension of this tract into more caudal levels of the spinal cord (i.e., into levels that control the hindlimbs) allowed movements of the fore limbs and hands to become independent of locomotor patterns or axial body movements (Heffner and Masterson 1983).

If independent movement of limbs did evolve from refinements and modifications of locomotor circuits, then one might expect some residual

manifestations of synchronized movements between right and left limbs, or between upper and lower limbs. In other words, it may be that instead of learning to coordinate the motions of right and left limbs, we actually learn to “discoordinate” them, to allow their independent movements (Marteniuk et al. 1984). Consistent with this idea, some studies have shown that reaction times decrease when subjects are permitted to react to a stimulus with both hands, instead of only one (Weisendanger et al. 1994; Kaluzny et al. 1994). It is also well known that rapid alternating limb movements are more easily made if both limbs are allowed to move together (Holmes 1917). Evidence for such “discoordinative” learning is also seen throughout ontogeny. For example, the earliest movements of infants tend to be rhythmic, stereotyped, and often bilaterally executed Thelen (1979, 1981a, b).

Three computational problems are immediately apparent when considering how the nervous system might coordinate patterns of muscle activation during the wide variety of possible independent movements of limbs. First, for any multi-joint movement in two or more dimensions, there are an infinite number of possible trajectories from any startpoint to endpoint. Thus, the sequence for muscle activation is not unique. Second, the nervous system must enact a compromise between specifying a movement before it begins (feedforward control), and guiding the movement using real-time sensory input (feedback control). This compromise must depend on the behavioral task being executed; for example, very fast movements necessarily rely entirely on feedforward control. Third, there is a tradeoff between planning a movement in external coordinates and how difficult it is to execute such a movement. Planning in terms of external coordinates allows the animal to accommodate for external constraints more easily, but execution then requires a transformation between external coordinates and joint coordinates and muscle activity.

Most independent movements of limbs are directed at external objects. Shifting posture and stretching need not be, but movements such as reaching, pointing, hitting, and kicking are generally directed at *something*, and these movements thus grade naturally into manipulation of objects. “Simple” forms of manipulation include pushing objects with the snout and forepaws (rats and dogs), or batting at a ball of string (cats); more complicated manipulations include grasping and the use of tools.

As diagrammed in Fig. 4, manipulation can be divided into two basic varieties that lie at different

positions along the spectrum of active somatosensation. First, as in use of tools, manipulation can simply *effect action*, while tactile perceptions remain subordinate. This situation is possible only if the object under manipulation is familiar to the animal, otherwise a period of exploration must precede successful manipulation. Second, an animal can manipulate an object to *explore* it or another object, in which case manipulation subserves the sensory system. Sensory input is clearly critical during both of these types of manipulatory movements.

Characteristics of exploratory movements

An animal’s exploratory movements are specifically directed towards acquiring information about the external environment. Animals can explore an object without manipulating it, and can manipulate a familiar object without exploring it. The physical properties of an object that may need to be sensed include position and orientation, size, shape, mass, compliance, brittleness, texture, friction coefficient, and temperature. Exploratory movements extracting these properties are in several ways different from the other types of movement so far discussed. The following characteristics of exploratory movements are independent of the particular sensory surfaces used for exploration. Exploratory movements:

- (1) *Are not patterned or stereotyped.* In most cases, the particular exploratory movement made is secondary to the information acquired by that movement. Klatzky and Lederman (1992) have shown that some *kinds* of movements are optimal for extracting particular types of information, but there remains a range of hand shapes and kinematics during these movements. Hardness of an object, for example, can be judged either by pressing down on the object with one finger, or by squeezing it between two fingers. As is the case for manipulation, there is no fixed pattern of muscle activation for exploratory movements; they can vary among individuals and for a single individual across trials.
- (2) *Do not require positionally accurate initial, intermediate, or final exploration points.* The points on an object at which exploration begins and ends are generally unimportant. Of far greater importance is that the explorer chooses sampling points that permit quick and accurate judgments about objects’ properties.

For example, an infinite number of combinations of points can provide information about curvature, as long as the points are spaced appropriate to the scale of the object. Judgments of temperature or hardness can be completely devoid of positional information. One exception to the rule that exploration does not require accurate positional information occurs when judging distances or spatial extent. In this case, it is clearly essential to have a sense for both initial and final positions.

- (3) *Are not particularly smooth.* Exploratory movements often involve abrupt changes in accelerations and velocities, and even discontinuities in contact with the explored surface. These non-uniformities imply that exploratory movements selectively “sample” parts of the object. Since only for very small objects can every point on the surface be touched, animals must maximize information from an under-sampled source. The sampling strategy thus involves not only choosing *which* points on the object to touch, but also selecting direction, force, and speed of movement. Some work has suggested that exploratory movements are slower over parts of the object’s surface where more accurate information is desired (Klatzky and Lederman 1992).
- (4) *Require central integration.* Unless the object being explored is smaller than the sensory surface (a rare case), information must be either spatially integrated from many sensory surfaces, temporally integrated from sequential activation of one sensory surface, or, the most usual case, both.
- (5) *Often require very fast feedback to appropriately adapt to unexpected sensory input.* Adaptive movements to unexpected inputs play at least two roles during exploratory behavior. First, because exploratory movements involve the investigation of unfamiliar objects, there is a high probability that either the animal or the object will become unstable. Sensory feedback, including reflexes, allows the animal to react to sudden changes in stability. Second, fast sensory feedback is essential for determining the subsequent exploratory strategy that will best extract the properties of objects. These sorts of strategies have been studied in detail by Lederman and Klatzky (1987).
- (6) *Are likely to be guided by multimodal feedback and may involve cognitive and/or attentional*

mechanisms. In addition to somatosensory feedback, exploratory movements are usually guided by other sensory modalities (e.g., vision, audition), and by memory. Cognition, attention, and memory are also clearly involved in such complex operations as recognition of objects; tactile exploratory behavior may in fact be said to culminate in stereognosis (the mental perception of the forms of solid objects by touch). It is therefore important to distinguish between these cognitive aspects of exploratory behavior and active touch proper (cf. Kalaska 1994). Active touch can be said to be limited to the cutaneous and kinesthetic sensations that arise during movements in which a sensory percept or intent dominates.

Relationships between active touch, exploratory movement, and sensorimotor prediction

Objective and subjective poles: the curious case of scratching

As described above, scratching and grooming are examples of self-generated passive touch. If you use the fingertips of your right hand to scratch the back of your left, very different sensations will be elicited in each hand. The dominant sensation will reside in the left (passive) hand, and you will have to concentrate hard to consciously perceive the sensations generated in the right. David Katz (1925, in Kruger 1989) described these differing sensations in active and passive surfaces as favoring “objective” and “subjective” poles. According to Katz, sensations favoring the objective pole are attributed to properties of external objects (e.g., the glass has a smooth texture, the book is rectangular). In contrast, sensations favoring the subjective pole are attributed to internal states, and remain essentially sensations. In the scratching example, then, information from the right hand is used to perceive the left as an external object, while information from the left hand is perceived as a scratching sensation.

Scratching and grooming thus occupy a unique position on the somatosensory spectrum, as they link active and passive touch, and consequently objective and subjective poles. Like locomotion, many forms of scratching behavior are thought to emerge from rhythmic spinal circuits (Baev et al. 1991). Like locomotion, scratching movements can be modified by ongoing afferent input (Baev et al. 1991). Unlike locomotion, however, the afferent input that modulates the scratching rhythm arises

from the surface *being scratched*. In other words, the afferent input that serves to modulate the central pattern governing movement need not arise from the actively moving body part: the goal of the active touch during scratching is to create a sensation in the immobile body surface. This idea receives support from a study by Berridge and Fentress (1986) who examined the effects of trigeminal deafferentation on the eating and grooming behavior of rats. Deafferented rats—missing all sensory input from lip regions—had trouble controlling tongue movements when eating, while forelimb movements remained unaffected. This would be unsurprising, but for the fact that during grooming behavior, deafferented rats had trouble controlling movements of the *forelimb but not of the tongue*. Thus, accurate forelimb movements during grooming depend critically on sensory input from the lip, while licking during grooming can occur in the absence of this sensory input. Grooming is an example of a situation, in which the sensory input from the passive sensory surface is required for the successful production of movement of a separate part of the body.

Active touch and sensorimotor contingencies

Humans are born with little volitional control of their muscles, and only gradually learn to execute the motor commands that result in a desired posture or movement. Movement, and its associated active somatosensation, must help an infant develop notions about causality in a fundamental way: the infant learns that when motor neurons are commanded to do X, the associated proprioceptors give response X'. Learning this causal relation would require the same movement to be made again and again. Thelen (1979) described 47 distinct rhythmic movements in normal infants, “including variations of kicking, rocking, waving, bouncing, scratching, banging, rubbing, thrusting, swaying, and twisting. The frequency and diversity of rhythmically repetitive movements are so great that the infant appeared to be following the dictum, ‘if you can move it at all, move it rhythmically.’” It seems therefore quite likely that the very first predictions an infant makes are about the proprioceptive input associated with a particular movement.

Externally generated passive touch is responsible for some of our most pleasurable (tickling, a caress) and most repulsive (insects crawling on skin) sensations. Although these reactions clearly involve cognitive mechanisms, there are strong perceptual (cf. the above discussion on objective

and subjective poles) and hedonic differences between sensory information acquired via our own movements, and sensory information acquired independent of movements being made. Externally-generated sensations may have the potential to elicit such strong emotions possibly because they bypass our fundamental notions of causality.

Specifically, passive touch can bypass our experience of cause and effect because it can be temporally unexpected. Active touch can easily be spatially unexpected, as when exploring an unfamiliar object, but it cannot be temporally unexpected. You might misjudge, or be surprised by, the physical properties of an object, such as texture, shape, weight, or temperature, but if you have set out to touch something you necessarily have an estimation of the time when you are about to touch it. Even when groping for an object in the dark, you have an expectation about when you might hit an object, and know immediately whether you have succeeded or failed. It is possible, then, that the rhythmic self-stimulating behavior that occurs under stressful conditions, such as rocking, rubbing hands together, or face tapping, is reassuring precisely because it links active and passive touch. The movement and associated somatosensation essentially add temporal causality into an otherwise unpredictable environment.

Proposed levels of sensorimotor prediction: hypothesis testing and control-level prediction

Based in part on our laboratory's work on the rat vibrissal system, we suggest that the exploratory process may consist of two levels of prediction operating in parallel. At the cognitive level, the animal may perform hypothesis testing about the identity or nature of the object. For example, the animal could form an initial hypothesis about the identity of an object, and choose an action or set of actions to test the hypothesis and thereby reduce uncertainty about that object. At a motor-control level, the animal must directly implement the set of motor actions required by the hypothesis test. For example, if testing a particular hypothesis requires the animal to “follow along the edge of an object until you reach a corner,” how might this actually be implemented? We suggest that these lower-level control sequences may themselves contain a predictive component, and use an example in the rat vibrissal system to illustrate these two different levels of prediction.

Hypothesis testing to determine the slope of a surface

An important feature of biological whiskers is their ability to extract three-dimensional (3D) features, either of solid objects or of flowing fluid. Two interrelated problems arise when using artificial whiskers to extract the shape of a 3D object. The first problem is *lateral slip*, in which the whisker slides out of its plane of rotation. Lateral slip makes it more difficult to use the moments (torques) at the base of the whisker to infer “radial object distance.” Radial object distance is the distance from the base of the whisker to the point where it contacts the object. The second problem is that the magnitude of lateral slip depends on the *coefficient of friction*. In general, this coefficient is not known and can vary greatly from object to object. We recently demonstrated a method to estimate radial object distance that includes passive accommodation for lateral slip along the object (Solomon and Hartmann 2008). The magnitude of lateral slip was shown to depend on the slope of the object’s surface at the contact point within the sensing plane (Fig. 5A) as well as on the frictional properties between the whisker and the object. To disambiguate the contributions of local surface slope and friction coefficient to the magnitude of lateral slip, we suggest that the rat may sample the same object at different orientations, as shown in Fig. 5B. Specifically, if the orientation of the whisker array can be tilted, whiskers can be performed against the object at a variety of orientations, effectively adjusting the relative slope of the surface. This amounts to

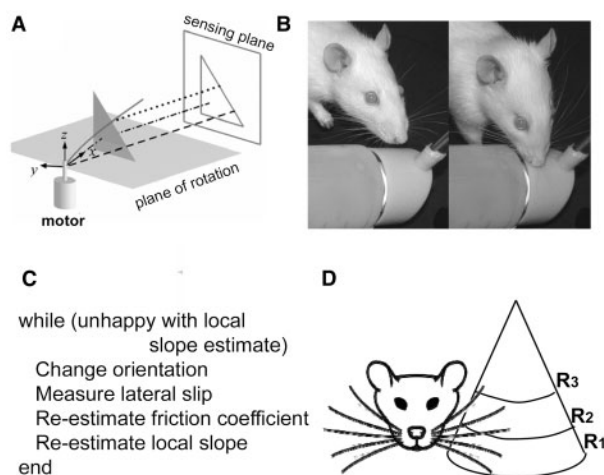


Fig. 5 (A) Lateral slip occurs as the whisker slips on the object out of its plane of rotation. (B) A rat’s typical exploratory sequences involve touching the same object from different orientations. (C) Proposed “while loop” for determining the local slope of a surface. (D) An example, in which each row of whiskers senses a different radius of curvature.

an in-field test of the object to determine the friction coefficient. Essentially we propose that the rat may implement the “while loop” shown in Fig. 5C, to perform tests of a set of hypotheses about the local slope of the surface.

Control-level prediction

Suppose that—to test a particular hypothesis about an object—the rat wishes to move its head and whiskers so as to follow along the edge of a surface. How might the animal ensure that it successfully performs this action? We suggest that these types of movements might be enabled by a set of lower-level (sub-cognitive) *control-level predictions* used solely for motor control. These predictions might be generated at the level of the brainstem and cerebellum, and would help the animal perform the motor actions required for fast and useful testing of hypotheses.

We specifically suggest that these control-level predictions may result from the relationship between spatial and temporal gradients of sensory data as the animal moves through the environment. The relationship between these gradients depends directly on the velocity of the moving sensory surface (e.g., the whisker array, or the primate hand). Computing spatial and temporal gradients at multiple scales would allow the animal to predict the stimulus that it will measure in the next instant (Gopal and Hartmann 2007).

Consider, for example, the case in which a rat is exploring an object in the shape of a cone (Fig. 5D). The radius of curvature sensed by the most dorsal row of whiskers is R_3 ; by the middle row, R_2 ; and by the most ventral row, R_1 . Within a given row, curvature is approximately constant, but across rows, the curvature changes gradually, from R_3 to R_2 to R_1 . Gradients of curvature can be combined with information about the velocity of the head to estimate the curvature that will be sensed at the next interval of time. This can be mathematically formalized as the complete derivative. If the environment is moving slowly relative to the head of the rat, the complete derivative for the curvature of the object in this example can be written as:

$$\frac{dk}{dt} = \vec{V}_{\text{head}} \cdot \vec{\nabla} \kappa \quad (1)$$

The idea represented by this equation is straightforward: During whisk N , the rat obtains information about curvature gradients across the array (κ). The rat then moves its head with velocity V_{head} . Consider three cases:

Case 1: The rat translates its head entirely in the upwards direction (dorsally) at a velocity V_{head} .

Taking the dot product of V_{head} with the gradient of the curvature will yield a prediction for how the curvature κ will change in the ventral-dorsal direction from whisk N to whisk $N+1$: namely, the most ventral whiskers will now sense a radius of curvature closer to R_2 , while the middle row of whiskers will sense a radius of curvature closer to R_3 . The most ventral row of whiskers will obtain new information, but the curvature gradient from R_1 to R_2 to R_3 can be extrapolated to predict that this new value should be R_4 , yet smaller than R_3 .

Case 2: The rat moves its head forward (roughly parallel to the surface of the cone) with a velocity V_{head} , so that each row of the whisker-array stays at approximately the same height as it was during the first whisk. Taking the dot product of V_{head} with the curvature gradient will yield a prediction of how the curvature κ will change in the caudal-rostral direction from whisk N to whisk $N+1$: namely, it will change very little. Because the curvature of the cone is constant at a given height, the rat will predict no change in curvature within a row at that height.

Case 3: The rat moves its head in an arbitrary direction, for example, in some combination of upwards and forwards. Again, the dot product multiplies the velocity by the curvature gradient in the appropriate direction, ensuring that the rat obtains an estimate for $d\kappa/dt$ consistent with the direction of the head's motion.

Computation of the gradients in equation 1 could in theory be implemented with standard "center-surround" receptive fields. This means that the prediction requires minimal central processing and could happen very quickly. In addition, it is easy to imagine that once having made the prediction, the nervous system could compare the predicted data with the actual data obtained. Movements enabled by this type of prediction could run independent of cognitive control unless there was a large difference between predicted and actual data. This type of "novelty" signal is consistent with reported cerebellar responses, seen particularly during exploratory behaviors and conditions of passive (temporally unexpected) touch (e.g., Gellman et al. 1985; Blakemore et al. 1998; Gao et al. 1996; Hartmann and Bower 2001).

Summary

Although not strictly necessary for the initiation and performance of movement, somatosensation is inextricable from smooth and accurate control of movement. Despite the importance of

somatosensation during all movement, somatosensations arising from movements with the goal of displacing a limb or external object have no name aside from "peripheral reafference." This relative anonymity belies the fact that somatosensory input is equally important when throwing a baseball as when judging the texture of a fabric.

Tactile sensations in which a sensory percept or goal dominates are called "touch," but the definitions of passive and active touch are not symmetric. Passive touch refers simply to the activation of exteroceptors on a sensory surface, when that surface is immobile. In contrast, the standard definition of active touch includes both exteroception and kinaesthesia, during movements whose goal is to generate sensation. Active touch is therefore often used synonymously with exploratory and manipulatory movements, but generally excludes manipulatory movements whose goal is to effect action (Gibson 1962).

We have provided a classification system for varieties of movement based on the role that somatosensory information plays during that movement. More specifically, the classification system is based on the recognition that an accurate definition of active touch requires the inclusion of both physiological and psychological variables: the *intent* of a movement is quite likely to influence the physiological responses associated with that movement. Thus, sensory signals may be quite different during two movements whose dynamics appear similar. This analysis suggests that it is critical to examine neural responses to sensory inputs over a wide range of behavioral contexts, as they are being differentially used by the animal.

The spectrum of active somatosensation ranges from movements that have almost purely displacement goals (locomotion), to movements in which sensory input dominates (exploration). Exploratory movements exhibit a set of characteristics that clearly distinguish them from other varieties of movement. Exploratory movements are unique in that the precise movement is secondary to the sensory information acquired by that movement. The exploratory process must further permit animals to extract identifying, invariant features of the object independent of the sequence of movements executed in the exploration of the object.

We have suggested that exploration of objects may consist of two complementary levels of sensorimotor prediction operating in parallel. At the cognitive level, the animal might move so as to perform *hypothesis testing* about the identity or nature of the object. The particular tests chosen by the

animal might be implemented in a manner that involves sequences of *control-level predictions* that could be generated at the level of the brainstem.

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