

Somatosensory input for real-world hand control

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Abstract

In this chapter, we consider how sensory feedback from the somatosensory periphery is integrated for the ongoing control of reaching, grasping, and object manipulation. We first review the peripheral neural basis of hand and arm control, specifically the signals arising from receptors embedded in muscles, tendons and skin. Then, in the context of recent behavioral and neurophysiological studies, we describe several prominent factors that make dealing with feedback signals in the context of real-world hand control particularly interesting: the hierarchical organization of feedback control loops, the need to integrate sensory inputs from multiple modalities in real-time, and the potential disconnect between perception and control.

Introduction

At the age of 19, Ian Waterman developed an autoimmune disorder that selectively destroyed the large-diameter afferent neurons below his neck that convey sensory information from his muscles, tendons, and skin. This rare condition effectively rendered him unable to move, not because he couldn't plan his actions or produce muscle force, but because his nervous system could not receive somatosensory feedback about the state of his body or about mechanical interactions with objects in the external world. Ian's story highlights the crucial role that somatosensory feedback plays in motor control, a role that is accentuated for dexterous actions like reaching, grasping, and object manipulation. Peripheral feedback is so essential for controlling the hand and arm that approximately 90% of the axons in the peripheral nerves of the upper limb transmit sensory information from the periphery into the central nervous system, while the remaining 10% of axons carry the motor commands from the central nervous system to muscles (Gesslbauer et al., 2017).

Studying sensory feedback forms one of the pillars of motor control research from the philosophical work of Descartes to the circuit dissection of Sherrington and ongoing through the present day. But sensory feedback was brought back into the spotlight of modern motor control research by Todorov and Jordan, who suggested that voluntary movement itself arises via the sophisticated manipulation of sensory feedback (Todorov and Jordan, 2002). The theoretical framework they introduced (but see, Loeb et al., 1990), based on optimal feedback control, aims to mathematically describe a motor action, like a reach, via a formal cost function that trades off the potential benefits and penalties associated with the execution of that action. The optimal reach, then, is the one that minimizes this cost function which, in turn, is implemented by adjusting the gains of feedback control loops over time. With certain cost functions, the optimal feedback control framework can reproduce many features of visually-guided reaching as well as many other tasks. It also provides insight into how the system should best integrate sensory feedback in real-time to achieve the task being performed. Because optimal feedback controllers only correct those errors that adversely affect task performance, observing how the nervous system responds to sensory inputs can provide evidence that the nervous system is doing something akin to optimal feedback control and provide clues as to the cost function that governs a particular action. Thus, in this framework, understanding how the nervous system processes sensory feedback is key to understanding motor control.

With optimal feedback control, the field appears to have a useful normative framework to understand motor behavior and some tentative links to the underlying neurobiology. Unfortunately, as it turns out, the mathematics of optimal feedback control are difficult even in simple scenarios and establishing firm links between optimal feedback control and behavior is hard because there exist many cost functions that can reproduce the same behavioral predictions. Moreover, a general scheme to make predictions about underlying neural circuits, say at the level of single neurons, remains more-or-less lacking. Luckily, there are heuristics as others have laid out in detail (Scott, 2004, 2016; Shadmehr and Krakauer, 2008). In this chapter, we stick to the level of heuristics and examine how sensory feedback rapidly contributes to reaching, grasping, and object manipulation. Although all sensory modalities can help support these actions, we primarily detail how the nervous system uses somatosensory feedback provided by receptors embedded in muscles, tendons and skin. We focus on real-world control in the sense that relatively naturalistic paradigms raise some specific issues including: (1) the hierarchical organization of feedback control loops and how this organization trades off computational flexibility for temporal delays, (2) how sensory feedback from multiple modalities is integrated in real-time and (3) the relationship between somatosensory feedback for perception versus motor control.

Peripheral neural basis of somatosensory inputs

Understanding the basic anatomy is always a good place to start, so we first describe the main somatosensory receptors for hand and arm control. There exist a variety of receptors embedded in the muscles, tendon and skin. These receptors signal information to spinal, brainstem and cortical processing centers, which all generate feedback responses. As we next describe, the signals arising from these receptors are more complex than typically appreciated and understanding how these signals contribute to hand and arm function remains a substantial challenge.

Proprioceptive inputs from the hand and arm

Muscle spindles are receptors embedded within, and running parallel to, the large extrafusal muscle fibers that generate muscle force. They are comprised of two types of intrafusal fibers: nuclear bag fibers and nuclear chain fibers. Large-diameter afferent nerve fibers (Type Ia) wrap around the non-contractile central portions of both types of intrafusal fibers, forming the primary sensory ending traditionally thought to signal information about dynamic and static muscle length. Smaller-diameter afferent nerve fibers (Type II) selectively wrap around the nuclear chain fibers, forming the secondary sensory ending traditionally thought to encode static length information. The distal portions of the intrafusal fibers are able to contract and are innervated by gamma motor neurons. Gamma motor neuron activity controls the contractile state of the intrafusal fibers, which modulates the spindles' sensitivity to muscle stretch but does not contribute appreciably to muscle force. Understanding the precise role of gamma motor neurons remains elusive (Windhorst, 2007), the simplest idea being that their activation is yoked to the activation of alpha motor neurons (which innervate extrafusal muscle fibers) so that the muscle spindle remains in its working range when its parent muscle changes length.

Golgi tendon organs (GTO) are sensory receptors that encapsulate 3-25 extrafusal muscle fibers and are arranged in series within the musculotendinous junction to signal the tension generated by a muscle. Each GTO is innervated by a large-diameter myelinated afferent fiber (Type Ib) that branches and interweaves through the tendon's loosely packed collagen fibers. When a muscle contracts, these collagen fibers straighten and compress the afferent axon, generating action potentials roughly proportional to muscle tension that are transmitted to the central nervous system.

Understanding the static and dynamic configuration of the body in space - the sense of proprioception - is obviously important for planning and executing actions and is often linked to muscle spindle activity. The direct connection between muscle spindles and proprioception likely stems from studies in animals and *ex vivo* preparations, which showed that spindle activity is correlated with muscle length and velocity - features that are also correlated with the position and velocity of the joint(s) that that muscle spans. Indeed, muscle vibration - which stimulates the muscle spindles - can cause illusory joint rotations (Eklund, 1972; Goodwin et al., 1972).

Recent work casts some doubt on a simple link between muscle spindle activity and proprioception because these receptors appear to encode other kinematic and kinetic variables besides length information. For example, in the cat, muscle spindle activity can encode the muscle forces that arise because of the mechanical properties of muscle cross bridges (Blum et al., 2017). Human experiments have long described a more complex mapping between muscle length/velocity and spindle activity in the context of active movement. For example, Dimitriou and Edin recorded from muscle spindle afferents while people grasped objects and pressed keys, two relatively natural hand actions, and found that spindle activity best predicts the future state of the parent muscle, and not instantaneous joint position or muscle length (Dimitriou and Edin, 2010). They suggested that muscle spindles operate as a forward sensory model that predicts the consequences of intended movement, acting as a peripheral mechanism to minimize the negative impact of sensory delays on controlling actions.

Cutaneous signals from the glabrous skin of the hand

Four distinct tactile afferent neurons innervate in the glabrous (i.e. hairless) skin of the human hand and fingers. These afferents collectively encode most of the critical information about the mechanical events that occur when interacting with and manipulating objects (Johansson and Flanagan, 2009). Fast-adapting-type-1 (FA-1) and slow-adapting-type-1 (SA-1) neurons innervate Meissner corpuscles and Merkel disks, respectively, both of which are located close to the skin's surface and are densely packed in the fingertips. Although both receptors respond to light touch, FA-1 neurons preferentially respond to high frequency skin deformations, like the moment an edge is contacted. SA-1 neurons, in contrast, can respond to steady-state indentations. Fast-adapting-type-2 (FA-2) neurons innervate Pacinian corpuscles, which are located in the deep dermal regions of the fingers and hands. FA-2 neurons are extremely sensitive and respond most vigorously to high-frequency transient events that occur when making or breaking mechanical contact with an object or surface.

Slow-adapting-type-2 (SA-2), already discussed above in the context of proprioception, innervate Ruffini endings embedded in the collagenous tissues of the dermis and respond to specific directions of skin stretch.

Most work investigating the function of tactile afferent neurons has focused on perceptions that arise when tactile stimuli are passively indented into the skin (Goodwin and Wheat, 2004; Johnson, 2001). These studies typically associate the four classes of tactile afferents, and their distinct anatomy and physiology, with non-overlapping functions based on correlations to perceptual phenomena or based on evoked percepts with specific stimulation protocols. However, there is substantial evidence that almost all real-world functions attributed to specific tactile afferents actually involve integration across multiple types of tactile afferent neurons (Saal and Bensmaia, 2014). For example, some textures, often those used experimentally, preferentially excite a particular class of tactile afferent neurons. However, the full spectrum of textures encountered during real-world actions recruits all types afferents and may even engage unique coding schemes - from spatial coding schemes that operate statically at low spatial frequencies to temporal coding schemes the require movement at high spatial frequencies. Determining how the nervous system integrates inputs across these afferents at various levels of the neuraxis remains an underserved area of study.

Studies investigating shape perception typically assume that tactile afferent neurons are distributed in a pixel-like array across the skin and that the spatial aspects of a stimulus, like edge-orientation or curvature, are represented in a veridical way - that is, the spatial layout of activated neurons provides a 'neural image' of the stimulus being indented into the skin. However, this conceptualization ignores a basic organizational principle of the somatosensory system, namely that tactile afferent neurons branch and innervate many mechanosensitive end organs. For example, each FA-1 neuron branches 4-6 times and innervates ~30 Meissner corpuscles (Nolano et al., 2003). As a result, tactile afferent neurons critical for resolving the spatial details of touched objects (FA-1 and SA-1s) have spatially complex receptive fields with many highly-sensitive zones and do not provide a veridical representation of a touched object or surface but rather emphasize some canonical features such as edge-orientation (Pruszynski and Johansson, 2014). An important question in the field is determining the evolutionary pressures that cause this peripheral complexity to arise, the limits of peripheral feature extraction, and how upstream neurons decode this information (Zhao et al., 2018).

Muscle feedback for posture and reaching: the hierarchical nature of feedback control

Real-world hand actions can be thrown off course because of noise internal to the motor system or by external forces, such as a bump by someone or something. One way the nervous system overcomes these challenges is by processing sensory information arising from muscle receptors and generating a series of rapid feedback responses (i.e. stretch reflexes) that engage multiple levels of the neural hierarchy including the spinal cord, brainstem and cerebral cortex.

The hierarchical organization of stretch reflexes and their underlying neural circuits have been extensively studied with much of the effort focusing on documenting functional differences between evoked responses at different latencies (for reviews, see Pruszynski, 2014; Scott, 2016; Shemmell et al., 2010). A common way to experimentally probe this neural hierarchy is to mechanically stretch a muscle and record a rapid set of phasic responses in an electromyogram (EMG) aligned on perturbation onset. It should be emphasized at the outset that, although such studies typically use relatively large mechanical perturbations since large perturbations evoke large reflex responses, such responses are still evoked when perturbations are on the scale of natural motor variability, suggesting that muscle feedback is continually processed in real-time to control our actions (Crevecoeur et al., 2012).

The standard view is that the hierarchical organization of fast feedback responses trades off temporal delays for computational sophistication: spinal circuits are quick but ‘dumb’ whereas cortical circuits are slow but ‘smart’ (**Figure 1**). The earliest feedback response - called the short-latency stretch reflex - manifests as a phasic wave of EMG activity 20-50 ms after perturbation onset. It is this reflex that a doctor is testing with their tendon hammer. Because of its latency, the short-latency stretch reflex almost certainly engages purely spinal circuits, most prominently a monosynaptic pathway linking primary muscle spindle afferents to motorneurons that project back to their parent muscle but also oligosynaptic pathways that can target other functionally related muscles (Pierrot-Deseilligny and Burke, 2005). In terms of function, the short-latency stretch reflex is typically thought to simply resist changes in muscle length and, consistent with this role, it is influenced by relatively low-level features of the stimulus or sensorimotor apparatus, like the amount and speed of muscle stretch or the state of the motorneuron pool.

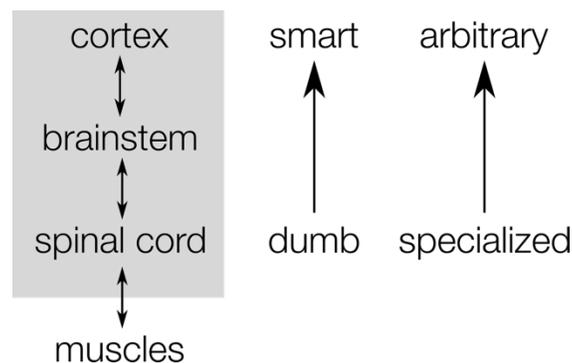


Figure 1. (Left) Cartoon of the nested feedback pathways that contribute to hand and arm control. (Middle) The traditional view is that the distinction between spinal and cortical feedback circuits relates to their functional capacity. (Right) An alternative view is that the distinction relates to the flexibility of these circuits, the spinal cord providing complex but relatively fixed functions driven by long-term evolutionary pressures and the cerebral cortex allowing for relatively arbitrary input-output relationships.

The next feedback response - the long-latency stretch reflex - manifests as a phasic wave of EMG activity 50-100 ms after perturbation onset. Given its latency, the neural basis of the long-latency stretch reflex has been a point of substantial debate, with some evidence favoring a transcortical pathway mediated by fast (Type Ia) muscle afferents and other evidence indicating a spinal pathway

mediated by slower (Type II) muscle afferents (Matthews, 1991). We now know that the long-latency stretch reflex reflects processing in spinal and cortical circuits, and that there are likely additional contributions via the brainstem, though relatively little is known in this respect (Shemmell et al., 2010). The key piece of evidence for a spinal circuit is that spinalized cats and monkeys still exhibit a clear long-latency stretch response (Ghez and Shinoda, 1978; Tracey et al., 1980). There are two key pieces of evidence for a transcortical pathway. First, corticomotorneurons in monkey primary motor cortex influence distal muscles of the limb and responded to mechanical perturbations at latencies early enough to contribute to the long-latency stretch reflex (Cheney and Fetz, 1984). In fact, cortical processing is not restricted to primary motor cortex as mechanical perturbations quickly evoke vigorous, yet selective, responses in parietal area 5, dorsal premotor cortex, and the supplementary motor area (Hummelsheim et al., 1988; Omrani et al., 2016). Second, patients with undesired bilateral movements, because of bifurcating corticospinal projections from primary motor cortex, show long-latency stretch reflexes in both limbs when muscles of one limb are stretched (Capaday et al., 1991; Matthews et al., 1990).

A remarkable aspect of the long-latency stretch reflex is that, even though it occurs with latencies substantially shorter than typical measures of voluntary reaction time, it exhibits many sophisticated features typically attributed to voluntary control processes: modulation by subject intent, sensitivity to task demands, engagement during decision-making and motor learning, routing of sensory information across muscles and effectors, as well as knowledge of the limb's dynamics and environment (for reviews, see Pruszynski and Scott, 2012; Scott, 2016). Perhaps the best real-world example of such functionality was demonstrated by Cole and colleagues who mechanically extended the thumb while participants were performing a pinching action as if to grasp an object (Cole et al., 1984). Unlike the short-latency stretch reflex, which was evoked only in the stretched thumb muscle, the long-latency stretch reflex was coordinated across thumb and finger muscles in a way that was supported accurate grasping. Although the presence of such sophisticated functional attributes is often attributed to the cortical circuits that underlie the long-latency stretch reflex, definitive links between particular attributes and specific neural circuits are rare and more work is definitely warranted.

The functional dichotomy between short-latency and long-latency stretch reflexes, as emphasized in the literature, makes it tempting to draw conclusions about how spinal and cortical circuits process somatosensory input for real-world control. But spinal circuits can drive many complex behaviors. A spinalized cat can be made to walk on a treadmill and can even change gait based on treadmill speed. A spinalized frog can swat noxious stimuli placed on its back and even account for different initial limb configurations. Indeed, the short-latency stretch reflex is not immutable. It is profoundly modulated at the transition from posture and movement as well as over the course of cyclical actions like gait and hand cycling. It can even change sensitivity with long-term learning when its magnitude is directly reinforced, a promising intervention for improving gait after spinal cord injury (Thompson et al, 2013). Thus, rather than contrasting spinal and cortical contributions according to their relative sophistication, a more accurate description of the hierarchy may relate to relative flexibility (Figure 1).

Whereas cortical circuits are able to transform sensory inputs onto motor responses in a seemingly arbitrary way, the spinal circuits support specific core functions of particular ethological relevance.

Taken together, fast feedback responses to mechanical disturbances are organized in a hierarchical fashion spanning the entire neuraxis. There are clear functional differences across this hierarchy. The long-latency stretch reflex, perhaps due to its transcortical contribution, is modulated by many, if not all, of the factors that influence voluntary control processes. The purely spinal short-latency stretch reflex is less flexible but can support some core functions or behaviors. One interesting aspect of this hierarchical organization that has received little attention is determining whether and how different levels of the hierarchy interact. Indeed, it is unknown whether and when longer feedback control loops predict how the shorter control loops are going to act, or whether each level of the hierarchy acts in isolation.

Reaching is automatically guided by visual and tactile feedback: integrating sensory inputs in real-time

People usually move their hands to touch an object and manipulate it in some way. In the real-world, objects can sometimes move, either because environmental forces are acting on them (e.g. someone bumps the table and a cup begins to fall) or because the object itself is an active agent (e.g. swatting a fly). Therefore, responding quickly when an object does move is a critical component of real-world reaching. Because information about object movement is often gathered visually, a great deal of work has investigated how unexpected changes in the visual location of a target elicits rapid feedback corrections of the hand's trajectory (Day, 2014; Gaveau et al., 2014). Such corrections occur without conscious awareness, leading to the idea that there exists an 'automatic pilot' of the hand with specialized neural resources - separate from those that initially generate the reaching action - acting to keep the hand moving towards its ultimate goal.

Vision is not the only modality that contributes information about the location of a reach target. In object manipulation and tool use, tactile inputs can be the main source of such information. Consider the many tasks where one hand is reaching towards part of an object held by the other hand: the cap of a bottle, a berry on a branch. Consider also the tasks where the reach target held in one hand is obscured by the digits of that hand: the clasp of a piece of jewelry, the hole in a small screw nut. In these cases, changes in the position of the target can be only detected through touch.

Recent work has examined whether tactile information about a handheld object also elicits relatively automatic corrections to keep the reaching hand on target (Pruszynski et al., 2016). Much like reaching for a berry while holding a branch, participants put the thumb of their left hand on a stick and made simple reaching movements with their right hand towards a ball mounted on the end of the stick. On a small proportion of trials, the stick suddenly rotated after participants had initiated their reach and the participant had to alter their reach trajectory to succeed at touching the ball. Critically, on some trials vision was occluded, so participants had to rely on mechanical events on their left thumb as well as some memory of the length of the stick. In other trials, participants did not

touch the stick with their left thumb but were given full vision, permitting a direct contrast of visually-guided and touch-guided reach corrections. Participants were readily able to perform both the tactile and visual tasks immediately, meaning the process did not require substantial learning or training. Both sensory modalities evoked similar rapid corrective responses appropriate for bringing the hand to the target. Changes in muscle activation were evident 75 ms after target jump and substantial kinematic deviations started about 110 ms after target jump. The latencies of the responses were not sensitive to the number of potential final target positions suggesting the action of a relatively direct feedback control mechanism.

What is the neural basis of such fast corrective responses and do rapid tactile and visual corrections share a common neural substrate? The similarity of these responses, particularly in terms of timing, suggest that this might be the case. Though little is known about the rapid tactile responses, the neural machinery of rapid visual corrections has been investigated in various animal studies as well as in patient groups. In cats, mid-flight adjustments to a sudden target jump are likely mediated by subcortical structures (Alstermark and Isa, 2012). In humans, rapid corrections are often attributed to the posterior parietal cortex based largely on the observation that patients with posterior parietal lesions are relatively normal at initiating actions but impaired at making fast corrective responses (Pisella et al., 2000). But work with a patient who has complete agenesis of the corpus callosum - a condition that eliminates direct communication between cerebral cortices - points to a brainstem pathway (Day and Brown, 2001). In this person, as expected of a purely cortical process, initiating a reach towards a target had greater latencies when the target was shown in the visual hemifield contralateral to the arm being used. However, as expected of a process that includes a subcortical contribution, correcting reach trajectories when the target suddenly jumped were the same regardless of how the target jumped or which hand was used. Although the ultimate subcortical pathway is unknown, work in monkeys has shown that the superior colliculus receives direct visual inputs and has a substantial population of neurons activated during reaching (Werner et al., 1997). Indeed, when carefully examining muscle activity relative to target jumps, the fastest response starting ~75 ms after target jump appears to be locked to the presentation of the target jump (Pruszynski et al., 2010) much like neural activity in the superior colliculus that causes express saccades (Dorris et al., 1997).

An important consideration when trying to integrate multiple sources of feedback is that the different modalities provide feedback information with different acuity and at different latencies. The classical solution to this problem in the perceptual and decision making literature is Bayesian estimation, whereby the input signals are combined in manner inversely proportional to their variance (Fetsch et al., 2013). Since visual information is almost certainly more accurate than tactile information in providing an estimate of the tip of a handheld object, the simplest formulation of Bayesian integration would suggest that visual information should dominate the overall response when both vision and touch are available. What does this extremely informative perceptual work tell us about real-world hand control? Perhaps not very much because the static Bayesian framework does not consider the fact that tactile information is available with substantially shorter latencies. Although these temporal differences can likely be ignored for perceptual processes that develop over seconds, in the context

of real-world hand control tens of milliseconds matter. As such, there may be substantial benefit to getting cruder sensory inputs now as compared to precise sensory inputs with some additional delay (**Figure 2**). Indeed, recent work suggests that, in the context of visually-guided reaching, the nervous system does not simply consider the relative acuity of the available sensory inputs but rather formulates a dynamical model that substantially penalizes delays (Crevecoeur et al., 2016). An important outstanding question relates to the underlying neural implementation of such a process and whether it can be implemented via subcortical structures or reflects the specialization of cortical machinery, as well as its relationship to the neural mechanisms thought to underlie static Bayesian estimation.

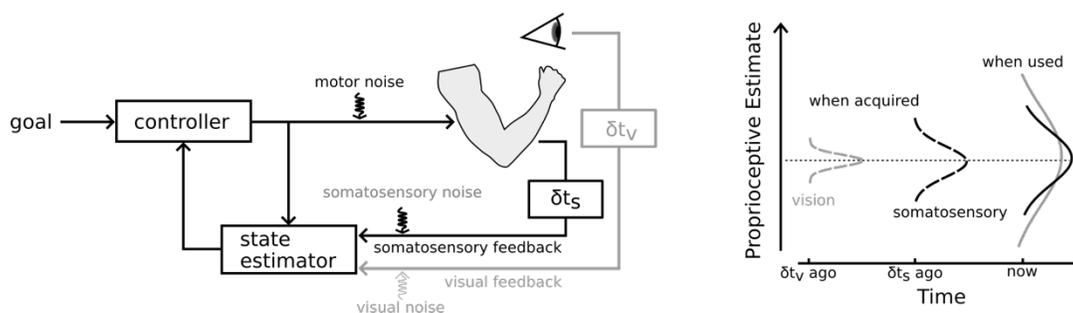


Figure 2. (Left) Diagram of a feedback pathway integrating visual and somatosensory inputs at different delays. (Right) Cartoon showing the influence of sensory delays on the veracity of visual and somatosensory inputs. Note that, although visual inputs are more precise at the moment of their transduction, the increased latencies associated with this pathway mean they provide a less precise estimate of hand position by the time the transduced information is processed for the purposes of hand control. Reproduced with permission from Crevecoeur et al., (2016).

Taken together, there exists a specialized system - perhaps subcortical in terms of neural implementation - that can update the details of an ongoing reach trajectory when the goal target position changes. Although this system is typically considered a specialization of vision and how visual inputs guide reaching, this seems unlikely to be the case as tactile inputs can drive similar responses at similar latencies. On the other hand, whether rapid visual and tactile responses are generated by the same neural circuit, and thus reflect part of the same control process, remains unknown. Clues could come from behavioral and neurophysiological experiments looking for the multi-sensory integration of visual and tactile inputs but such comparisons need to be cognizant of the inherent limitations associated with porting ideas about static Bayesian integration from perceptual studies into the domain of motor control.

Tactile feature extraction during hand control: generalizing from perception to control

Putting on a necklace often requires pinching a small clasp and aligning it with an even smaller ring. In this and many other real-world manipulation tasks, executing fine control of the hands and digits requires that the nervous system has fast and accurate access to information about each object's orientation. Such tasks are often done in the absence of vision, either because the action is done out of sight (e.g. behind the head) or because the objects themselves are so small that direct vision

is obscured by the digits. In these situations, information about an object's orientation is largely based on how its edges activate mechanoreceptors in the glabrous skin of the fingertips. Events which degrade the tactile signals generated via the mechanoreceptors, such as prolonged cold exposure or peripheral nerve injury, degrade or even preclude fine manual dexterity.

Given its importance in the real-world, it is not surprising that a wealth of studies have investigated edge-orientation processing. In most of these studies, the experimenter pressed an edge or a series of edges into the participant's fingertip and asked the participant to make some judgement about the orientation of the edge or the relative orientation of multiple edges. Edge-orientation acuity as measured in these perceptual identification and discrimination tasks develops on the timescale of seconds and ranges between $\sim 20^\circ$ degrees for long edges that span the whole contact surface of the finger (Bensmaia et al., 2008). For short edges on the order of a few millimeters, akin to the necklace clasp and ring, edge-orientation acuity is very poor, approximately 90° (Peters et al., 2015).

The speed and acuity of tactile edge-orientation processing as reported in these perceptual studies is far too slow and crude to support many aspects of dexterous manipulation. Recent work has investigated edge-orientation acuity directly in the context of a simple object manipulation task (Pruszynski et al., 2018). Rather than ask participants to report edge-orientation directly, the experimenters asked participants to touch and rotate a randomly oriented dial towards a pre-specified target position. Critically, information about the dial's initial orientation could only be extracted by touching a raised edge on the dial's surface. Thus, extracting edge-orientation information was not an explicit feature of the task, as in perceptual assays, but rather an implicit component of the object manipulation task being performed. Participants performed remarkably well in this task - nearly an order of magnitude better than in perceptual studies. On average, they were able to orient the dial within 3° of the target orientation for long edges spanning their entire fingertip and remained impressive even for very short edges (e.g. 11° for a 2 mm long edge).

Not only were participants exceptionally accurate but they gathered tactile edge-orientation information very quickly, within ~ 130 ms of initially contacting the edge and well before they had reached a steady level of contact force. Using tactile information so quickly is consistent with the automaticity by which tactile signals are used in other aspects of manipulation, including mechanisms supporting grasp stability. In fact, participants never used all their available time nor did the fidelity of the sensory information (in this case, the edge length) influence the latency or timing of dial rotation. This points to a relatively low-level feedback control scheme and contrasts with many perceptual or decision making studies showing that reaction time measures increase as the veracity of the sensory input decreases.

Several factors likely account for the speed and acuity differences in tactile processing for perception versus motor control. One explanation is that there may exist more information when the participant is actively engaged with an object, perhaps due to subtle differences in contact dynamics. There are also differences in experimental timing that may put more stress on memory systems in the context of perceptual studies. For example, forced choice paradigms present stimuli sequentially, requiring

the participant to hold information about the first presented stimulus in memory in order to make a judgement about it relative to the second presented stimulus. Memory decay in many real-world manipulation tasks is minimized because the action is initiated quickly after the object is contacted and because contact is maintained during execution.

It is also possible that the difference between tactile processing for perception and control reflects substantive differences in their underlying neural mechanisms. Indeed, a large number of studies have shown that the processing of sensory information is sensitive to task and context. Perhaps the best example comes from the visual system, where it is well established that visual inputs are differentially processed for motor and perceptual tasks and that such differences reflect the engagement of specialized visual processing pathways in the cerebral cortex (Milner and Goodale, 2006). The ventral visual pathway extracts detailed semantic information about objects, supporting perception, cognition and memory. The dorsal visual pathway builds a pragmatic representation of objects in the environment, supporting real-time motor actions and guiding behavior. An equivalent segregation for the sense of touch has not been studied with equivalent protocols. For example, no one has directly tested whether the same tactile stimuli recruit different neural pathways depending on whether the acquired sensory information is used for perception or control.

Perception and control may also be served by different neural codes at the level of the peripheral apparatus. The currently accepted model supporting tactile acuity is built on a long tradition, starting with Mountcastle, of comparing neural responses to some set of stimuli in monkeys with perceptual reports from monkeys or, more often, from humans using similar stimuli (Johnson, 2001). This formulation starts with the notion that tactile afferent neurons have simple Gaussian sensitivity profiles. That is they respond most robustly at the center of their receptive field and progressively less towards the margin. At the population level, the receptive fields of many tactile afferent neurons overlap and spatial details are resolved based on the relative firing rates of neurons with nearby receptive fields via some neural interpolation scheme (Saal et al., 2017; Wheat et al., 1995). Although this approach does well at explaining perceptual phenomena, a key weakness of such an intensity coding scheme is that estimating the firing rates of individual neurons takes a substantial amount of time and thus appears too slow to underlie hand control.

An alternative model that could support tactile acuity for hand control starts with the fact that human and monkey tactile afferent neurons branch in the skin and innervate many spatially distinct mechanoreceptors, yielding spatially complex receptive fields with multiple zones of high sensitivity (Johansson, 1978; Suresh et al., 2016). Since these complex receptive fields are highly overlapping, at the population level it means that an edge at a given orientation will excite one subset of first-order tactile neurons whereas an edge at a different orientation will excite some other subset of first-order tactile neurons (Pruszynski and Johansson, 2014). In this formulation, the degree to which differently oriented edges synchronously engage different subsets of neurons determines edge-orientation acuity (**Figure 3**). Such a coincidence code can yield high acuity and potentially operates at the time scale of the first incoming action potentials. Moreover, there exist established neural mechanisms for

processing such a code based on the massive divergence and convergence of first-order tactile neurons onto second order neurons in the cuneate nucleus.

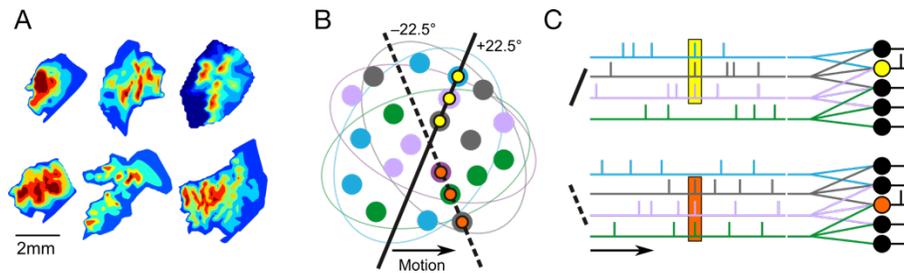


Figure 3. (A) Exemplar receptive fields for first-order tactile neurons. (B) Cartoon showing how complex receptive fields can temporally structure spiking outputs and (C) how upstream neurons can read out this orientation based on the coincidence of action potentials across the population of first-order tactile neurons. Reproduced with permission from Pruszynski and Johansson (2014).

Taken together, there is a functional and perhaps neurophysiological distinction between how tactile information is processed for perception and control. Determining the degree of these functional differences and the precise neural mechanisms that underlie them is an important avenue for future research. For example, appreciating these differences could improve brain-machine interfaces trying re-inanimate hand function by ‘writing-in’ somatosensory information into the brain (Bensmaia and Miller, 2014). The biomimetic stimulation protocols currently used are largely based on neural responses inspired by perceptual studies which, in the worst-case scenario, are orthogonal to the neural code that typically serves control.

Conclusion

The goal of this chapter was to describe how somatosensory information is critical to real-world hand control. We focused on three specific issues: the hierarchical organization of feedback control loops, how sensory feedback from multiple modalities is integrated in real-time, and the relationship between somatosensory feedback for perception versus motor control. These three topics were not meant as an exhaustive list. Rather, these examples were meant to serve as templates for thinking about how naturalistic tasks reveal behavioral and neural insights that can go unseen from within any particular laboratory paradigm.

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