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Primer

Neural adaptation

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The term ‘neural adaptation’ refers to the common phenomenon of decaying neuronal activities in response to repeated or prolonged stimulation. Many different roles of adaptation in neural computations have been discussed. On a single-cell level adaptation introduces a high-pass filter operation as a basic element for predictive coding. Interactions of adaptation processes with nonlinearities are key to many more computations including generation of invariances, stimulus selectivity, denoising, and sparsening. Neural adaptation is observed all the way along neuronal pathways from the sensory periphery to the motor output and adaptation usually gets stronger at higher levels. Non-adapting neurons or neurons that increase their sensitivity are rare exceptions. What computations arise by repeated adaptation mechanisms along a processing pathway? After giving some background on neural adaptation, underlying mechanisms, dynamics, and resulting filter properties, I will discuss computational properties of four examples of serial and parallel adaptation processes, demonstrating that adaptation acts together with other mechanisms, in particular threshold nonlinearities, to eventually compute meaningful perceptions. Python code and further details of the simulations illustrating this primer are available at https://github.com/janscience/adaptationprimer.

Neural adaptation is a ubiquitous phenomenon that can be observed in many neurons in the periphery as well as in the central nervous system, in vertebrates as well as in invertebrates. The response of an adapting neuron, measured as a firing rate, a membrane voltage, or a calcium signal, declines in response to a prolonged or repeated presentation of a stimulus (Figure 1). The stimulus can be a sensory stimulus, an injected current, a light-activated construct like channelrhodopsin, or any other condition the experimenter can apply or evoke in a repeated manner. In this broad definition, neural adaptation is a phenomenological description of a common property of neural responses with no implication of a specific mechanism or functional role. Behavioral adaptations, in contrast, are adaptations in the function of a whole organism. Neural adaptations at one stage of neural processing usually are not directly related to the final output.

Any neuron sensitive to the applied stimulus responds with some initial or onset response to a simple step stimulus, for example a playback of a pure tone of constant intensity or the deflection of a whisker by a fixed amplitude (Figure 1A). A non-adapting neuron, a tonically spiking neuron, would keep firing with this rate. The adapting neuron, however, decreases its response activity down to some steady-state value. In a phasic neuron, spiking activity is even completely abolished. Most neurons show phasic-tonic responses: they lower their firing rate in response to constant stimulation, but keep responding to the stimulus. Many neurons traditionally classified as tonically spiking neurons do in fact mildly adapt their firing rate as in the example shown in Figure 1A. The transition from tonic over phasic-tonic to phasic response types is a gradual one, reflecting a gradual increase in the strength of the underlying adaptation process. The stronger the adaptation, the lower the steady-state response.

Adaptation mechanisms

The reduction of the response of a neuron to a constant stimulus indicates inhibitory mechanisms operate as the underlying adaptation processes that counteract the stimulus. On the single neuron level, these are various voltage- or calcium-gated ionic currents that are directly or indirectly activated by high membrane voltages, in particular during action potentials. For example, voltage-gated calcium channels open during each action potential and calcium flows into the cell. Calcium-activated potassium currents are activated that act subtractively on the input current and therefore inhibit the

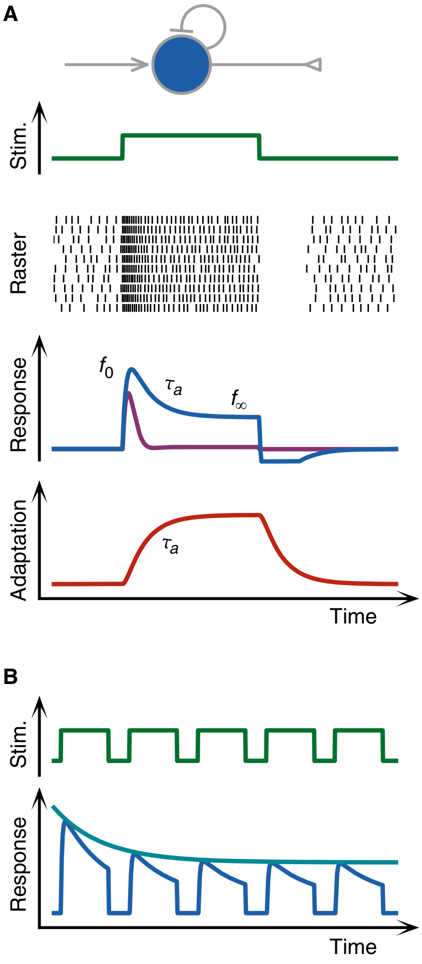

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Figure 1. Neural adaptation.
(A) In a single neuron, adapting responses are caused by intrinsic ionic currents that self-inhibit the neuron depending on its activity (indicated by the inhibitory feedback loop). The response — the firing rate (blue) of a spiking neuron (raster) or the membrane voltage of a non-spiking neuron — to a step stimulus (green) is highest right after the onset of the stimulus (f_0) and then decays down to a lower steady-state value, f_∞. This decline is caused by the slowly increasing adaptation level (red) driven by the enhanced activity of the neuron. The time course of the adaptation process is governed by the adaptation time constant τ_a. Note that after switching off the stimulus, spiking is initially inhibited because of the enhanced level of adaptation at the end of the stimulus. During the absent or strongly reduced activity the neuron recovers from adaptation and returns to its baseline activity. Neurons with stronger adaptation display more phasic responses (purple). (B) Adaptation to a pulse train (green). Within each pulse neural activity (blue) adapts. This adaptation accumulates over successive pulses (indicated by the cyan line) if the neuron does not completely recover from adaptation between the pulses.

generation of action potentials. Note that an increase in spiking threshold associated with adaptation is an epiphenomenon of such adaptation currents, but not a primary cause of adaptation (Benda *et al.*, 2010). These output-driven mechanisms all self-inhibit the neuron. Input-driven adaptation mechanisms, on the other hand, already inhibit the input before it is translated into changes in the membrane potential or in neuronal firing. Short-term depression of the input synapses or all sorts of adaptation mechanisms in sensory transducer cascades are examples of input-driven adaptation.

On the network level, combinations of excitatory connections between neurons with inhibitory ones form a rich substrate for neuronal adaptation. While the excitatory connections convey the stimulus, the inhibitory connections counteract the excitatory inputs on slower timescales. Lateral and presynaptic inhibition are basic network motifs contributing to neural adaptation. In this primer, I highlight a few network motifs that illustrate how adaptation contributes to different kinds of computations and how the role of adaptation depends on the computational context.

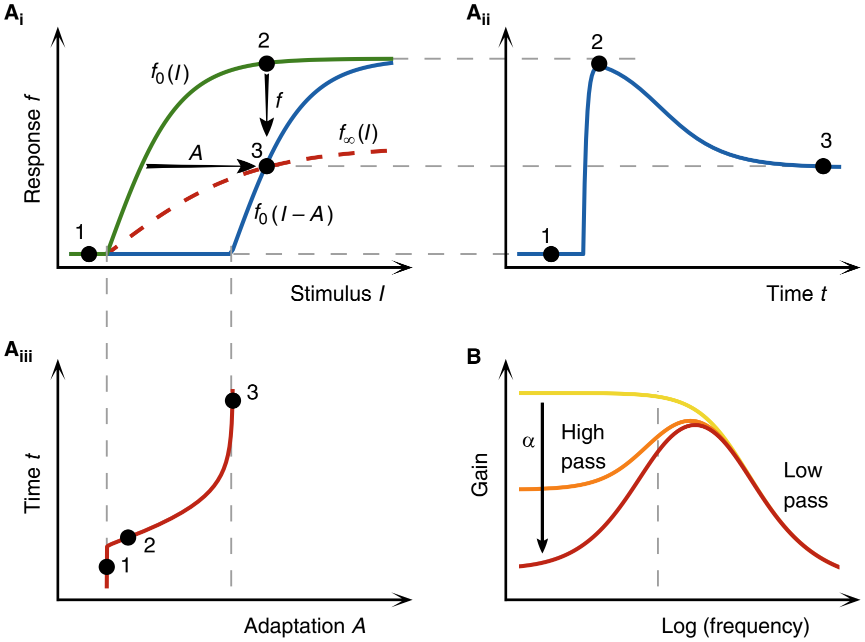

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Figure 2. High-pass filter properties of adaptation.
(A) Subtractive adaptation shifts (horizontal arrow) the neuron's non-adapted response function, $f_0(I)$, by the current adaptation level *A* to higher stimulus intensities *I*. This shifted response function $f_0(I–A)$, which does not change its gain, governs the transmission of stimulus components that change on faster time scales than the adaptation dynamics. In the absence of a stimulus, the firing rate response (ii) and the adaptation level (iii) are zero (black dot 1). Immediately after switching on a fixed stimulus (black dot 2), the firing rate response is given by the non-adapted response function, $f_0(I)$, and the adaptation level is still close to zero. Driven by the increased firing rate of the neuron, the adaptation level increases approximately exponentially (iii). This shifts the response function to the right (horizontal arrow) and as a consequence the firing rate response decreases (vertical arrow and ii). The adaptation process reaches a steady-state once the shifted response curve intersects the steady-state response curve $f_\infty(I)$ at the current stimulus intensity (black dot 3). The steady-state response curve governs the transmission of stimulus components slower than the adaptation dynamics. The stronger the adaptation mechanism, the lower the steady-state response curve and the smaller its gain. Note that the deviations from an exponential decay of the firing rate in (ii) result from the non-linear shape of the response curves in (i). (B) By shifting the response function to the current mean stimulus, subtractive adaptation implements a high-pass filter. The stronger the adaptation mechanism (α, arrow), the more attenuated are low-frequency components of the stimulus by the reduced gain of the steady-state response curve. The cutoff frequency of the adaptation high-pass filter (dashed line) is set by the inverse adaptation time constant. Independent of the adaptation mechanism, responses to higher frequency components are attenuated by the low-pass filter caused by the membrane time constant or the firing rate.

Dynamics

At its core, neural adaptation is a dynamic process. In particular, it is an interplay between a fast process, the response of a neuron to some excitatory input, and slower, inhibitory adaptation processes. On which time scale the adaptation processes evolve and how they relate to the timescales characterizing the excitatory input is decisive for the functional role of adaptation.

To a first approximation, the decay of the firing rate in response to a constant stimulus is exponential and can be described by an adaptation time constant. Neural adaptation phenomena differ widely in adaptation time scales. In auditory systems, for example, rapid adaptation is associated with time scales in the millisecond range, whereas in visual systems, 'rapid' adaptation typically evolves on time scales of many hundred milliseconds up to seconds. Using longer stimuli reveals that neural adaptation usually involves additional processes with longer adaptation time constants in the range of seconds or even minutes that further reduce the response. Often, the time course of adaptation in response to constant stimulation resembles that of a power law, possibly composed of many exponential processes with distinct time constants. In contrast to exponential adaptation, power-law adaptation is not bound to a specific time scale in the stimulus and plays an important role in generating speed-invariant responses (Clarke *et al.*, 2015).

Filter properties

Neural adaptation, a decay of the response to a constant stimulus, is a fingerprint of a high-pass filter (Benda and Hennig, 2008). Low-frequency stimulus components are suppressed by the adaptation dynamics. The decaying response of an adapting neuron to a step stimulus illustrates this (Figure 2A). Let us assume that the neuron initially is not adapted and that in the absence of a stimulus the neuron is not firing. Switching on a stimulus in a step-like manner is a quick, high-frequency change

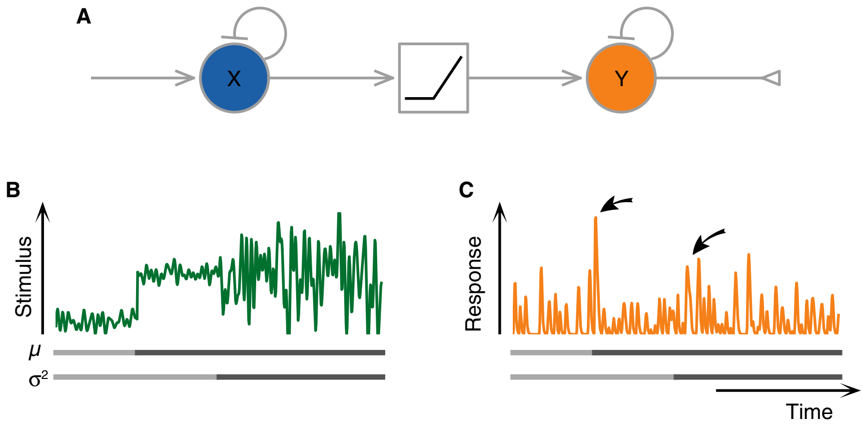

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Figure 3. Adaptation to the mean and the variance.
(A) Two-stage adaptation with a threshold nonlinearity in-between. The first neuron (*X*) subtractively adapts the response to the mean stimulus amplitude by shifting its response curve appropriately to higher stimulus values. The second neuron (*Y*) after the nonlinear transformation adapts the response to the variance of the stimulus in a divisive manner. In contrast to neuron *X*, this neuron does not shift its response curve, it scales it down. (B) First, the mean stimulus amplitude μ is stepped up, and then the stimulus variance σ^2 is increased as indicated by the gray shading of the horizontal bars. (C) The response of neuron *Y* to the fast components of the stimulus is largely independent of these changes in stimulus mean and variance, except right after the transitions (arrows).

in stimulus intensity. The adaptation process is too slow to react to this sudden change and thus the neuron responds strongly with a high firing rate (Figure 2A$_{ii}$) as characterized by its unadapted input–response curve $f_0(I)$ (or 'f–I curve' firing rate versus input, Figure 2A$_i$). After the step the stimulus stays on a constant level. Driven by the activity of the neuron the adaptation level *A* increases exponentially to a higher level (Figure 2A$_{iii}$). In the example illustrated, the adaptation level acts subtractively on the stimulus and thus shifts the f–I curve to the right: $f_0(I–A)$. The further the f–I curve moves to the right, the more the response of the neuron is reduced until the adaptation level reaches its steady-state value. The corresponding firing rate is given by the steady-state f–I curve, $f_\infty(I)$, which describes the fully adapted responses for each stimulus value.

High-frequency stimulus components that change on time scales faster than the adaptation time constant are transmitted with a high gain given basically by the slope of the unadapted f–I curve (Figure 2B). Low-frequency or constant stimulus components that change on time scales slower than the adaptation time constant are transmitted with a reduced gain given by the slope of the steady-state f–I curve. They result in only small changes in the output firing rate of the neuron. The larger the adaptation strength the lower this gain, the stronger the high-pass filter induced by the adaptation process. Note that even faster stimulus components are also low-pass filtered by other processes like the membrane time constant or the finite firing rates of a neuron.

Adaptation to stimulus mean and variance

Natural stimuli are not just switched on and off, as in many experiments, but they usually change gradually in time. Sound or light intensity as transduced by hair cells or photoreceptors in natural scenes, for example, are not constant but continuously fluctuate on various time scales and within some distribution of intensity levels. During the day, mean light intensities are much higher than during dusk or dawn, and several adaptation processes in the eye adapt the visual system to these changes. On a faster time scale, similar changes in mean light intensity happen when stepping from an open meadow into the woods. In addition to changes in mean stimulus level, higher-order statistics, like variance or temporal correlations, also change when roaming through an environment. Many neurons continuously and gradually adapt their responses to such dynamical changes in stimulus statistics (Fairhall *et al*., 2001). Adaptation to both the mean and the variance of a stimulus can be explained by a two-stage adaptation process with a threshold nonlinearity in-between (Figure 3A) — both in insect auditory systems (Clemens I., 2018) and visual systems (Kastner and Baccus, 2014). The first adaptation process adapts the response to the slowly changing mean input by filtering out low-frequency components. By cutting off negative values of the remaining zero-mean signal, the threshold nonlinearity converts changing variances of the input in changing mean values. The final adaptation stage then again adapts to this mean value, this time not by shifting the response curve, but by scaling it along the input axis. This is known as 'divisive adaptation' — the dynamic range of the neuron is adapted to the input variance. As a result, the response of the neuron is independent of both the mean and the variance of the input signal (Figure 3B,C).

This example nicely illustrates how, even in a simple feed-forward circuit, neural adaptation is not just enhanced as we go from one stage to the next. Rather, nonlinear transformations process the signal and subsequent adaptation then works on the resulting transformed signal. This way the different adaptation stages then add different computations to the overall pipeline. Nonlinear processes can be found everywhere in neural systems. Both synaptic transmission and action potential generation implement threshold nonlinearities and voltage-gated ionic currents in dendritic trees, for example, might transform the input in nonlinear ways, too.

Adaptation to the mean and variance of a sensory stimulus are a simple form of predictive coding. For example, mean light intensities usually change slowly such that they can be well predicted. This is what the adaptation level encodes: it is the low-pass filtered input and thus follows the slow changes of the sensory stimulus only (Figure 2A$_{\mathrm{iii}}$). The adaptation level is subtracted from the input and in this way the response of an adapting neuron encodes the fast changes that cannot be predicted. The resulting high-pass filter (Figure 2B) attenuates the response to slow, predictable changes in the stimulus. See Weber *et al.* (2019) for an in-depth review on adaptation and its relation to coding principles.

Stimulus-specific adaptation

Let us now turn to circuits with adaptation processes in parallel branches. Stimulus-specific adaptation is a common phenomenon that has been extensively studied in auditory systems of both mammals and insects (Whitmire and Stanley, 2016). When recording the response of a single neuron in the auditory cortex, for example, while repeatedly stimulating with an acoustic stimulus, the neuron responds with a high firing rate to the first presentation of this stimulus; the response then adapts during subsequent presentations of this ‘standard’ stimulus (Figure 4A). The response to interspersed ‘deviant’ stimuli, however, is still large — it is not adapted. For this to work, the deviant stimulus must differ from the standard stimulus in some feature, for example in its sound frequency. The non-adapted response to the deviant stimulus would be impossible if adaptation took place close to spike generation in the recorded neuron, because the spike generator would adapt to all stimuli exciting the neuron in the same way. For stimulus-specific adaptation, the adaptation process must take place in distinct pathways that separately process and specifically adapt the different stimuli. This can be input neurons to the recorded neuron (Figure 4B), which in turn might inherit some of the adaptation from more peripheral neurons, or distinct branches of the dendritic tree of the recorded neuron. The input pathways need to differ in their tuning curves to the stimulus feature of interest and the standard stimulus should not excite the pathway processing the deviant stimulus (Figure 4C,D). Only then can the system specifically adapt to the standard stimulus and not to the deviant.

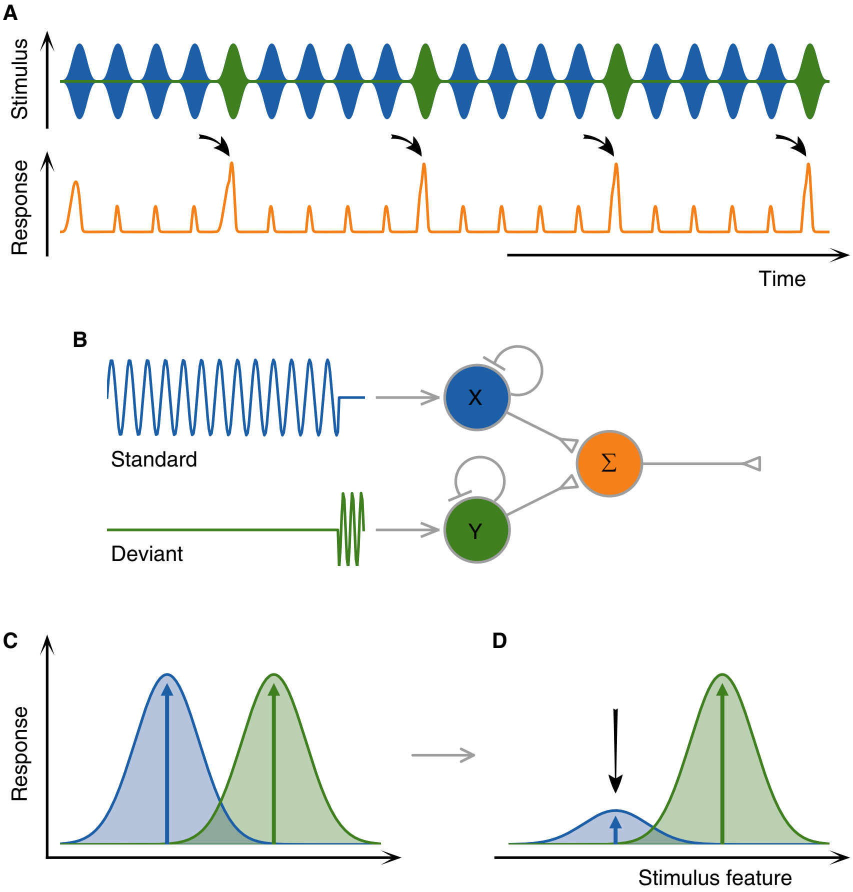

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Figure 4. Stimulus-specific adaptation.
(A) A standard stimulus (blue) is presented repeatedly, whereas a deviant stimulus is presented at longer intervals only. The stimuli differ in some feature, for example in their sound frequency in case of auditory stimuli. The response of a sensory neuron to the first standard stimulus is strong but then adapts to subsequent presentations of the standard stimulus. However, the response of the rarely presented deviant stimulus is still large; it is not affected by the adaptation to the standard stimulus (arrows). (B) This stimulus-specific adaptation can be explained by two input neurons, *X* and *Y*, that differ in their tuning properties (bell shapes in C and D) and thus specifically adapt to their preferred stimulus. The output neuron sums up the responses of both input neurons. (C) Initially, the output of the two input neurons and of the output neuron is strong (upwards arrows) for both stimuli, because the input neurons are not adapted yet and thus their tuning curves have full amplitude (bell shapes). (D) After presenting the standard stimulus for some time, the input neuron tuned to this stimulus feature adapts (downward arrow) and the output response decreases. The neuron tuned to the deviant stimulus is not adapted and still conveys a strong response.

Stimulus-specific adaptation shifts the overall tuning of the output neuron away from the stimulus feature of the standard stimulus (Figure 4D). This property could explain perceptual biases and a number of aftereffects in optical illusions, like for example the waterfall illusion (Whitmire and Stanley, 2016), where neurons tuned to downward movements are adapted when fixating a waterfall for a while. When looking away from the waterfall the whole scenery seems to move upwards. Because the responses of downward-neurons are reduced, they cannot balance out the unadapted responses of neurons tuned to upward movements and the perception is thus biased to an overall upward movement.

While the circuitry for stimulus-specific adaptation shown in Figure 4B conveys the basic principle, it certainly is an oversimplification. First of all, often more than just two

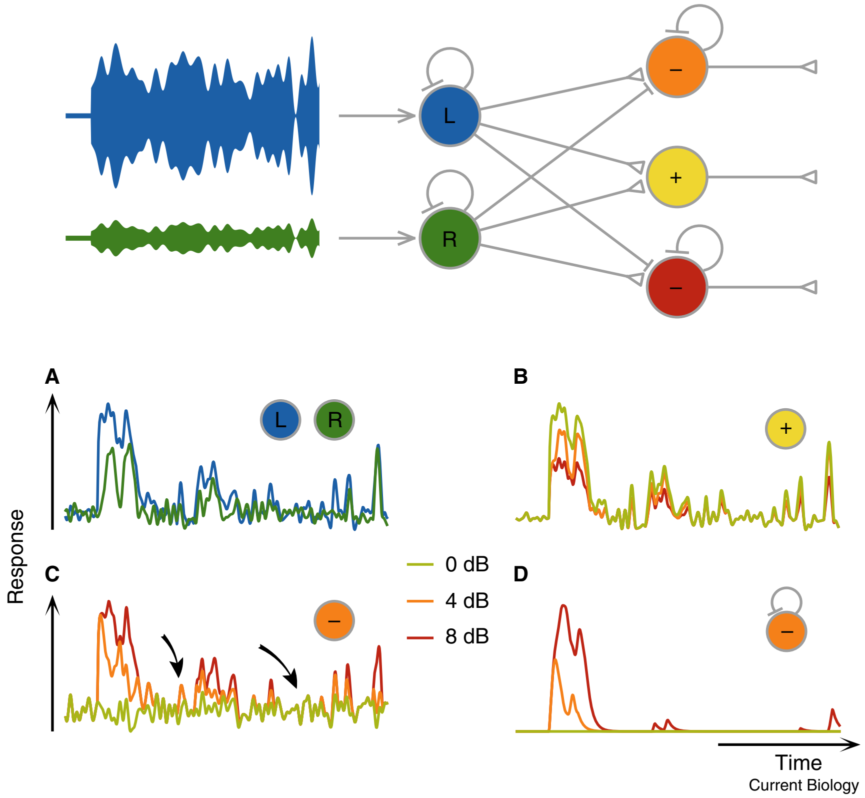

Figure 5. Resolving ambiguities.

An auditory system receives an acoustic stimulus on the left (*L*) and the right (*R*) ear. Depending on the direction of the sound source, the input to the contralateral ear is attenuated relative to the one to the ipsilateral ear (legend in C). (A) The input neurons adapt their responses by shifting the response curves to the prevailing sound intensity. (B) A pattern encoder (+) sums up the activity of both input neurons. Its response is mostly independent of sound direction (all three responses align) after an initial adaptation process. (C) Subtraction of the two inputs by a sound-direction encoder (–) reveals directional information (responses are ordered according to sound direction/attenuation of sound on contralateral ear). This response is, however, quite noisy (arrows) after the initial adaptation subsided. (D) Additional intrinsic adaptation in this neuron removes these non-informative responses but keeps the most informative initial response. By means of this additional intrinsic adaptation process a robust code for sound direction is ensured.

pathways converge onto the output neuron. The mammalian auditory system, for example, has more than two frequency channels. In this way, the output neuron maintains sensitivity to rare and thus interesting sounds, but reduces its response to ongoing background sounds of whatever frequency. Also, as already mentioned above, all sorts of adaptation processes along the input pathways contribute to stimulus-specific adaptation. In particular, specificity of the input pathways could be enhanced by lateral inhibition between the input channels.

Resolving ambiguities

As we have discussed in the context of Figure 2, adaptation primarily suppresses low-frequency components of the input. This is a desired operation to make the output invariant with respect to some slowly changing stimulus features. On the other hand, removing low-frequency components makes the response ambiguous. The absolute value of the input can no longer be uniquely inferred from the neural response. For example, a 100 Hz firing rate of an auditory neuron could have been evoked by a soft 30 dB SPL (sound pressure level) sound in a quiet room, or by a 80 dB SPL sound on a 50 dB SPL loud background. If the absolute sound intensity is of no behavioral relevance, then adapting the input early on in the auditory pathway is a viable option. But when both the absolute and the relative sound intensity are relevant, then peripheral adaptation would be detrimental for encoding absolute sound intensity.

Such a conflict has been studied in the auditory system of grasshoppers (Figure 5, Hildebrandt *et al*., 2015) and very similar constraints might be at work in the mammalian auditory system as well. Grasshoppers are both interested in encoding the temporal pattern of a perceived grasshopper song for assessing species, sex, and fitness of the singer, as well as in localizing the song. Sound localization in grasshoppers is entirely based on inter-aural level differences, because inter-aural time differences are simply too small. In order to compute inter-aural level differences, central neurons would need to subtract absolute sound levels from both ears. Ideally, auditory receptors should not adapt to sound intensity in order to convey absolute sound intensities. On the other hand, processing the temporal pattern benefits from adapting the dynamic range of each ear to the different mean sound intensities. A central pattern encoder would then simply add up the inputs from both sides. In fact, even the peripheral auditory neurons adapt (Figure 5A), favoring pattern encoding by a central neuron that adds up the inputs from both ears (Figure 5B).

What about sound localization? Is this still possible, even though absolute sound intensity is already adapted away in the periphery? Simply subtracting the information from the two ears indeed results in ambiguous responses (arrows in Figure 5C); directional information is heavily deteriorated. Right after the onset of the stimulus, however, the responses from the two ears are not yet adapted and indeed convey information about absolute sound intensity and thus sound direction. Adding intrinsic adaptation to the sound-direction encoder, with the adaptation time constant matched to the one of the periphery, restricts its response to episodes when the periphery is not adapted and thus conveys information about absolute sound intensity (Figure 5D). Otherwise the intrinsic adaptation silences the neuron and this way ensures that only informative inputs excite the neuron.

With noiseless neurons and with linear response curves that extend over the whole relevant range of sound intensities, coding of both sound pattern and sound direction would be no problem at all, no matter whether the input neurons adapt or not. The need for the input neurons to adapt arises because of their limited dynamic range. This limited dynamic range and additional neuronal noise makes it difficult to retrieve directional information from the input neurons when simply subtracting their activity. In that sense nonlinearities — the nonlinear, saturating response curves of the input neurons — limit the capabilities of the system. A smart utilization of adaptation at different stages of the pathway makes up for the limitations imposed by such nonlinearities.

Generating sparse codes

A main goal of sensory systems is to transform the dense and continuous representation of sensory information in the periphery to a code that is better accessible for higher order processing and generating behaviors. One common strategy is to make the representation more sparse, such that only a few neurons are activated by very specific stimulus features. The orientation tuning of neurons in V1 of the visual systems, the coding of song features in the HVC nucleus of song birds, and the encoding of odors by Kenyon cells in insects are prominent examples of sparse representations. While the efficient coding hypothesis faithfully predicts such sparse codes in many different neural systems, the neuronal mechanisms that lead to a sparse code are less well understood.

Betkiewicz *et al*. (2020) have shown that both cell intrinsic adaptation and lateral inhibition contribute to the formation of a sparse code for odors in Kenyon cells of the insect mushroom body. Each Kenyon cell receives input from a subset of the olfactory glomeruli *via* projection neurons (neurons *X* and *Y* in Figure 6). This input leads to a dense code because many Kenyon cells respond tonically to the presented odor (Figure 6A). Intrinsic adaptation currents in the Kenyon cells make this response temporally sparse. The response is strongest at the stimulus onset (Figure 6B). Lateral inhibition on its own makes the response spatially sparse. The baseline response of non-excited neurons is suppressed (Figure 6C). Both intrinsic adaptation and lateral inhibition lead to a temporally and spatially sparse representation of the odor that is encoded by a brief period of spiking activity of a few neurons (Figure 6D). This demonstrates how several adaptation mechanisms together contribute to implementing efficient codes.

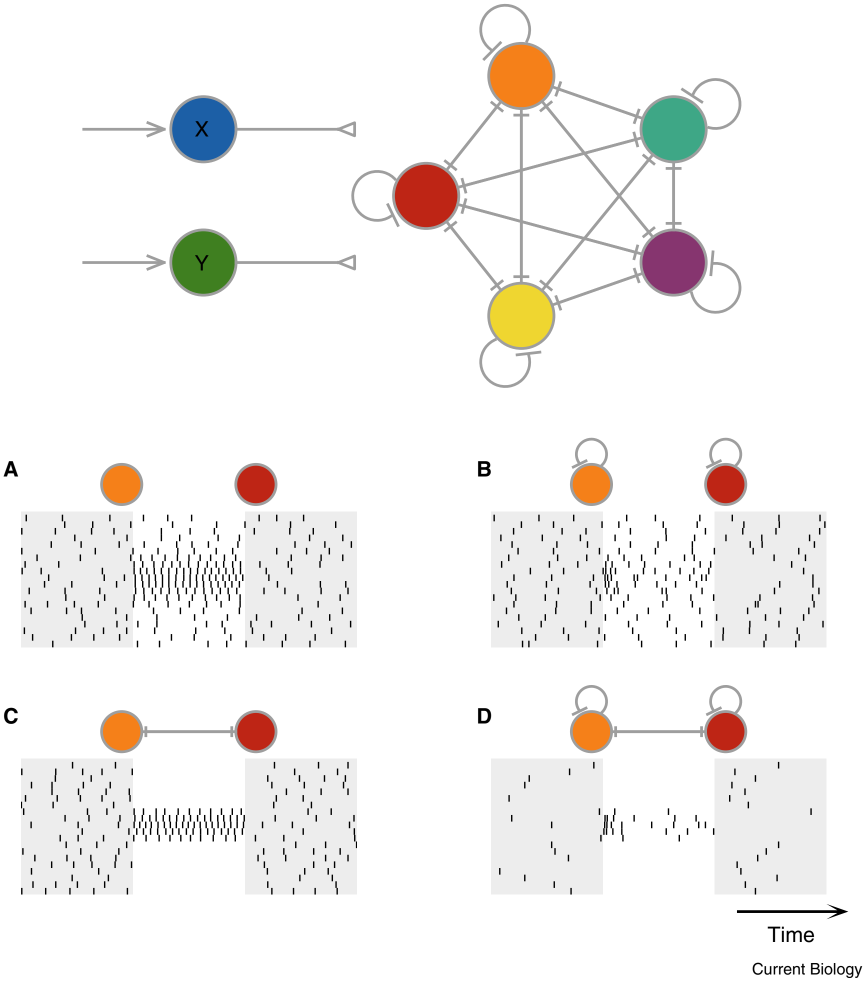

Figure 6. Generation of a sparse code.
A low-dimensional input (neurons *X* and *Y*) is expanded into a high-dimensional and sparse feature code in a network of neurons with intrinsic adaptation and reciprocal inhibitory connections. (A) Without inhibition and adaptation, the population response (raster) to the stimulus (white background) is neither spatially nor temporally sparse. All neurons are firing throughout the stimulus presentation. (B) Intrinsic adaptation generates temporal sparseness by emphasizing the stimulus onset. (C) Reciprocal lateral inhibition ensures spatial sparseness by inhibiting the spontaneous activity of the non-stimulated neurons. (D) By means of both mechanisms a sparse code is created. A specific stimulus is encoded by only a few neurons with only a few spikes.

Summary

The four examples that I have discussed of the functional role of neural adaptation emphasize that adaptation should be viewed in its computational context and not as a specific computational function. The many adaptation mechanisms provide various forms of slow inhibition that together with nonlinearities provide a rich toolkit for neural systems to perform computations — not only in sensory systems. Observing neural adaptation on every level of a processing hierarchy does *not* imply that the input is high-pass filtered over and over again. Rather, the interplay with threshold nonlinearities transforms the code such that on every stage neural adaptation might play a different functional role. In particular, subsequent adaptation does also not imply that information about absolute stimulus levels is entirely lost. As we have seen, absolute levels can be preserved and enhanced in epochs right after the onset of a stimulus. Neural adaptation is one of many components used for neural computations to extract and detect behaviorally relevant aspects of the sensory environment in order to generate meaningful behaviors. Adaptation time scales are adapted to the stimulus statistics and matched to other adaptation mechanisms in the circuit. Understanding the roles of adaptation along a pathway is a key component of understanding how and why the neural code is transformed along the pathway.

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Snaps of a tiny amphipod push the boundary of ultrafast, repeatable movement

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Surprisingly, the fastest motions are not produced by large animals or robots. Rather, small organisms or structures, including cnidarian stinging cells, fungal shooting spores, and mandible strikes of ants, termites, and spiders, hold the world acceleration records[1–5]. These diverse systems share common features: they rapidly convert potential energy — stored in deformed material or fluid — into kinetic energy when a latch is released[4–6]. However, the fastest of these are not repeatable, because mechanical components are broken or ejected[5,6]. Furthermore, some of these systems must overcome the added challenge of moving in water, where high density and viscosity constrain acceleration at small sizes. Here we report the kinematics of repeatable, ultrafast snaps by tiny marine amphipods (*Dulichiella* cf. *appendiculata*). Males use their enlarged major claw, which can exceed 30% of body mass, to snap a 1 mm-long dactyl with a diameter equivalent to a human hair (184 µm). The claw snaps closed extremely rapidly, averaging 93 µs, 17 m s^{-1}, and 2.4 x 10^5 m s^{-2}. These snaps are among the smallest and fastest of any documented repeatable movement, and are sufficiently fast to operate in the inertial hydrodynamic regime (Reynolds number (Re) >10,000). They generate audible pops and rapid water jets, which occasionally yield cavitation, and may be used for defense. These amphipod snaps push the boundaries of acceleration and size for repeatable movements, particularly in water, and exemplify how new biomechanical insights can arise from unassuming animals.

Amphipods (Peracarida) are small-bodied crustaceans that include familiar ‘beach hoppers’ or ‘scuds’ and are widespread in salt- and fresh-water environments. In many, the first two thoracic limbs are claw-like structures, or gnathopods (Figure 1A), which exhibit diverse forms for feeding, grooming, aggression, and mating[7]. Many second gnathopods are also sexually dimorphic: enlarged in males and likely used for male–male competition, mate acquisition, and copulation[7]. Among amphipod genera with sexually dimorphic claws, *Dulichiella* stand out: males possess a single, massively enlarged second gnathopod that can exceed 30% of total body mass, and can snap closed so quickly as to defy visualization[8,9].

To characterize the kinematics of ultrafast snaps, we collected male amphipods of *Dulichiella* cf. *appendiculata* by hand from algae on floating docks at the Duke Marine Lab (Beaufort, NC, USA). Live males were attached to a custom filming apparatus to precisely position their strikes during high-speed imaging (300,000 frames per second, 256x128 pixels, 2.33 µs shutter). We digitized landmarks on 60 strikes from 16 individuals to quantify kinematics (see Supplemental Information). In preparation for snapping, males first cock the dactyl open at approximately 70° (Figure 1C). The dactyl then swings rapidly closed, causing the entire claw to recoil violently. The quickest snaps occurred in less than 50 µs (Table S1), which is 10^4 times shorter than an average eye-blink.

Amphipod snaps rival the speeds and accelerations of the smallest and fastest systems known (Figure 1B)[5,6]. Average linear acceleration of amphipod snaps (2.4 x 10^5 m s^{-2}) is similar to the maximum linear acceleration of smashing mantis shrimp strikes. Systems that are lighter and exhibit higher accelerations than amphipods are not repeatable (that is, they can only fire once), including cnidarian stinging cells and fungal ballistospores. Mandible strikes by some ants and termites are repeatable, faster, and accelerate similar mass as amphipods (Figure 1B), but their mandibles move through air rather than water. Nematode jumps are repeatable and launch a lighter mass, yet their accelerations are orders of magnitude slower. Therefore, amphipod strikes exhibit an exceptional combination of features — one of the smallest, fastest, *and* repeatable mechanical systems yet