

2017

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Daizaburo Shizuka

University of Nebraska-Lincoln, dshizuka2@unl.edu

Eileen Hebets

University of Nebraska - Lincoln, ehebets2@unl.edu

Kim L. Hoke

Colorado State University, kim.hoke@colostate.edu

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Shizuka, Daizaburo; Hebets, Eileen; and Hoke, Kim L., "Neural Circuitry for Target Selection and Action Selection in Animal Behavior" (2017). *Papers in Behavior and Biological Sciences*. 82.

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Published in *Integrative and Comparative Biology* 57:4 (2017), pp 808–819.

doi 10.1093/icb/ix109

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Published September 26, 2017.

From the symposium “Integrating Cognitive, Motivational and Sensory Biases Underlying Acoustic and Multimodal Mate Choice” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

Neural Circuitry for Target Selection and Action Selection in Animal Behavior

Kim L. Hoke,¹ Eileen A. Hebets,² and Daizaburo Shizuka²

¹ Department of Biology, Colorado State University, 1878 Campus Delivery,
Fort Collins, CO 80523-1878, USA;

² School of Biological Sciences, University of Nebraska–Lincoln,
Lincoln, NE 68588, USA

Corresponding author — Kim Hoke, email Kim.Hoke@colostate.edu

Abstract

Animal behaviorists have long strived for a comprehensive understanding of the proximate and ultimate causes of complex behavior, and we propose that recent advances in neurobiology can help reshape or clarify this behavior-oriented understanding. We begin with an overview of current views of neural circuit mechanisms that mediate target selection and action selection. In target selection, different stimuli compete for priority in sensory-motor processing. Action selection is the process by which multiple possible motor actions compete for priority in a manner which balances the needs of the animal with opportunities or threats in the environment. We next discuss spatial and temporal aspects of target and action selection, highlighting how neurophysiological responses to complex displays depend on spatial and temporal components of multisensory stimuli. We use two examples—(1) spatial attention as an example of target selection in the vertebrate midbrain and (2) goal-directed locomotion as an example of action selection in the insect central complex—to further clarify neural circuit dynamics as they relate to target and action selection, and their interaction. We suggest that a deeper understanding of neural circuit properties will introduce new hypotheses into behavioral studies, especially those aimed at understanding the evolution of complex displays based on receiver sensory biases. Additionally, knowledge of neural circuit properties can elucidate ways in which current context and previous experience can together modify neural circuit dynamics to produce complex context-dependent behavioral responses that often characterize animal behavior.

Introduction

Understanding how animals translate sensory inputs into motor outputs has been the holy grail of animal behavior since early ethologists initiated their first studies (e.g., Tinbergen 1951). This process of sensory-motor integration is inherent in nearly all aspects of animal behavior, including mate choice, foraging, agonistic interactions, or anti-predator tactics. Although behaviorists recognize that animal behavior reflects sensory-motor integration, the details of this integration are frequently treated as a black box, despite recent advances in studies of neural circuitry. Much ongoing behavioral research still relies implicitly and solely on classical frameworks of sensory-motor integration, which view behavioral outputs as the general consequence of neurons accumulating sensory information until they surpass a threshold, which then triggers a behavioral response (e.g., Castellano et al. 2012). While multiple conceptual frameworks exist for aspects of this process (e.g., Green and Swets 1989; Blumstein and Bouskila 1996; Sherman et al. 1997; Mendelson et al. 2016), many of the details leading to behavioral responses remain abstract. Meanwhile, modern advances in neurobiology have elucidated general principles by which structural arrangements and electrophysiological dynamics within neural circuits can inform our understanding of the mechanisms linking sensory processing to behavioral output.

We propose that incorporating realistic features of neural circuitry and its dynamics into studies of animal behavior can facilitate our understanding of the diversity and flexibility within behavioral systems and can provide insight into the context dependence of sensory-motor processing. A better understanding of neural circuitry could guide behaviorists in generating testable hypotheses, innovative experimental designs, interpretations of results, and importantly could open up a dialog between behaviorists, neurobiologists, and psychologists (among others) that could aid in the advancement of all three fields. To this end, we provide an overview of neural circuit architecture and function with reference to how it might apply to research in animal behavior. We briefly review our current state of knowledge regarding neural circuit dynamics and discuss how neural circuit architecture facilitates the interacting processes of target and action selection. We describe well-studied animal systems to provide detailed examples of both target and action selection and explicitly discuss spatial and temporal aspects of neural circuitry. Throughout, we highlight how neural

circuit dynamics might inform an understanding of animal behavior and animal decision making.

Target and action selection within neural circuits

Animal behavior, regardless of the context in which it is realized, comprises a series of sensory-guided actions during which the nervous system accomplishes two major tasks: target selection and action selection. Target selection (or stimulus selection) is the process by which sensory regions dedicate energetically expensive neural activity to an especially salient subset of the external world (Dutta and Gutfreund 2014). Action selection is the process by which neural circuits activate a single motor program from among the many possible (Prescott et al. 2007). Thus, target and action selection together allow the animal to produce a single cohesive behavioral response based on multiple cues in the environment (Fig. 1), whether that response is to accept a courting suitor, to attack a particular prey, or to flee a predator. We highlight target and action selection as widespread, and possibly ubiquitous, neural phenomena. These processes could contribute to cognitive traits such as those underlying judgment and decision making (Mendelson et al. 2016), and we advocate that a deeper understanding of these target and action selection processes will help distinguish impacts of sensory filtering and sensory-motor integration on higher level cognitive tasks such as discrimination or categorization.

Many animals exhibit sensory-triggered behaviors in which dedicated small neural circuits identify targets in the environment using sensory filtering such that the activated sensory neurons only represent a relevant subset of the external world. Such sensory filtering is hypothesized to mediate rapid, reflex-like escape behaviors (e.g., Roberts 1992; von Reyn et al. 2014) as well as responses to conspecifics, which is particularly well-documented in insects (reviewed in Nityananda 2016). In such instances, selection among targets in the environment is based on relatively simple computations in the circuit. The first, or highest amplitude, stimulus simultaneously (1) initiates an action and (2) suppresses competing actions to produce a single coherent behavior. This simultaneous initiation of one action and suppression of others accomplishes a basic form of action selection that prevents the animal from attempting two incompatible motor programs. But what happens when the situation is more complex?

We focus primarily on complex neural circuits in which numerous sensory neurons represent a broad range of sensory stimuli which could initiate or modulate various different categories of behavioral responses (mate choice, foraging, etc.). During target selection, both across and within sensory systems (e.g., visual and olfactory), sensory neurons responding to different stimuli in the environment compete against one another for priority in subsequent stages of sensory processing. Additionally, sensory inputs from salient targets can modify circuits that mediate action selection (see **Fig. 1**). Similarly, within action selection circuits, neurons representing possible motor programs compete for priority based on factors such as internal needs (e.g., hunger, reproductive condition), history (e.g., recent cues indicating high predation risk), and diverse sensory inputs (e.g., multimodal cues/signals) (reviewed in Cisek 2007). We are interested in understanding the processes underlying behavioral responses in these realistic scenarios where animals are faced with multiple potential sensory targets in the environment as well as multiple potential actions.

Because the integration of sensory processing and behavioral output involves complex interactions between numerous elements, computational modeling is often required to explore how different circuit dynamics influence this system. Computational approaches employing models grounded in the neuroanatomy and physiology of well-studied neural circuits have identified general circuit features that mediate the competition among possible targets and possible actions (e.g., Lai et al. 2011; Cisek 2012; Sridharan and Knudsen 2015). Two essential features of target- and action-selection circuits are: (1) lateral inhibition, in which activity in one group of neurons inhibits the activity of comparable neurons associated with other stimuli or actions; and (2) recursive circuitry, including features such as feedforward and feedback loops. Dynamic patterns of activity in circuits with lateral inhibition and recursive circuitry support the competitive processes by which a single target or single action emerges over time from among the possible neural firing patterns to produce the ultimate output behaviorists often observe and study (reviewed in Gold and Shadlen 2007). To better illustrate the circuit dynamics underlying target and action selection, we discuss detailed examples that highlight spatial and temporal features of neural processing. These examples demonstrate that animal behavior may engage multiple sub-circuits that contribute to target or action selection in parallel and that fundamental neural processes bias the likely activity patterns within neural circuits.

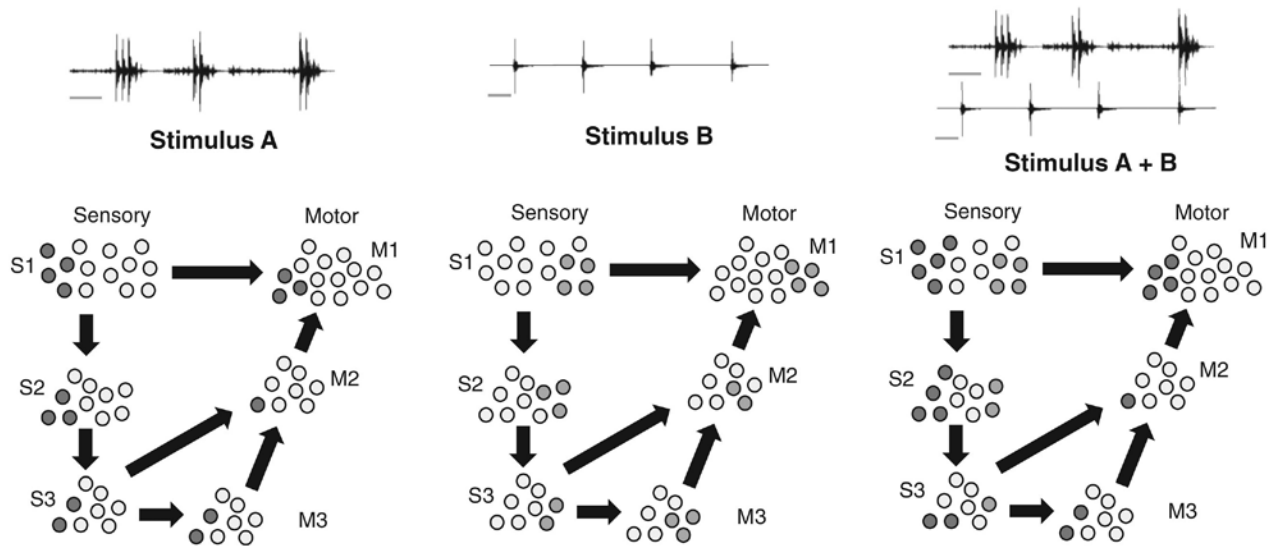


Fig. 1. Generic circuit highlighting hierarchical circuits that mediate the sensory-motor transformations involved in context-dependent complex behaviors. Each circle represents a neuron, and these neurons are grouped into brain regions (labeled S for largely sensory regions and M for largely motor regions). The block arrows represent major anatomical projections between brain regions. Sensory stimuli such as vibrational stimulus A and B excite neurons in sensory region S1 (indicated by the dark circles). This early stage of sensory processing acts as a relay to higher sensory centers S2 and S3, where a subset of neurons that receive strong inputs are also activated (dark circles). These sensory regions interact with premotor areas involved in motor planning (M2 and M3) and motor execution areas (M1 in this example) to implement sensory-triggered behaviors. Such sensory-motor links occur at multiple levels of the sensory-motor hierarchy, which supports complex network interactions and complex behavioral outputs. We highlight that different sensory stimuli might activate distinct motor programs that would produce diverse observable outputs (e.g., vocalization, approach, and attacks). When two stimuli are present simultaneously, sensory processing may be biased toward one stimulus (stimulus A in this example) via the process of target selection. This process then biases action selection, the process by which only one motor program is planned and executed. Complex context dependence of behavioral response can arise due to neuromodulation at all stages of this circuit, as well as feedback loops (e.g., projections from M3 or S3 to S1 that alter early stages of sensory processing based on recent stimulus history, physiology, and other contextual or environmental features).

Spatial aspects of target and action selection

Whether trying to identify landmarks for navigating home, to assess particular attributes of a courting suitor, to successfully transfer food into the gaping mouths of one's offspring, or to identify the parasitic

egg that does not belong in one's nest, animals must attend to relevant stimuli coming from particular locations in their environment. As these stimuli are processed, target and action selection involve a complex network of neurons that inherit the spatial components of the sensory modalities upon which they are based. These spatial aspects of sensory systems are egocentric: changing head position or body orientation immediately changes the part of the external world from which stimuli induce electrical changes in the sensory neuron. Thus, the sensory motor transformations that underlie animal behavior are implemented within the context of the spatial maps specific to the sensory systems and behavioral responses (reviewed in Barron and Klein 2016). Some aspects of complex behaviors that involve assessing potential mates or competitors may in fact be related to sensory-motor processing directed toward a specific location rather than a weighting attributes assigned to a particular individual.

The neural circuit dynamics described above depends on both the spatial layout of receptors within a modality as well as the connectivity between modalities. For example, vision is inherently spatial: each photoreceptor responds to light from a particular part of the external world, and visual processing depends on comparisons of light responses among adjacent photoreceptors across time. In vertebrates, the spatial pattern inherent in photoreceptor arrays is translated through many stages of visual processing, whereas the spatial details erode rapidly in some of the early visual interneurons in insects (Wu et al. 2016). Similarly, pressure and mechanosensory processing areas are also spatially organized in vertebrates, with comparisons among adjacent receptors on the skin critical for discriminating details of objects in space.

Other aspects of sensory processing require neural computations to pinpoint spatial origins of stimuli. Insects such as the stick insect, *Carausius morosus*, use mechanosensory information sensed by antennal receptors for orientation, extracting information about nearby objects in space based on movements of tactile hairs and proprioceptive responses to deflection at the antennal base (e.g., Ache and Dürre 2013, 2015). Fish brains calculate the sources of water vibrations by comparing excitation of adjacent lateral line receptors on the body (Coombs et al. 1996). Insect and lizard ears highly directional, responding almost exclusively to sound coming from one hemisphere (Römer and Krusch 2000; Christensen-Dalsgaard and Manley 2005), while the auditory systems of birds and mammals extract the precise location of

sound sources by comparing amplitude and timing differences of vibrations arriving at the two ears (reviewed in Carr and Christensen-Dalsgaard 2016). Determining the sources of volatile chemical cues involves more complex comparisons of chemical gradients in space and time (e.g., Khan et al. 2012).

Potentially salient stimuli throughout the environment continuously compete for representation within the animal's higher order sensory systems through target selection. One way in which relevant stimuli can win this competition is through selective spatial attention, or the focusing of sensory processing to a specific location in the environment. Extensive research has shown that directing sensory attention toward one location in space allows animals to respond more rapidly to, and process more detailed information about, stimuli in that part of the world (reviewed in Knudsen 2007). Selective spatial attention is potentially most intuitive for visual systems, but should be relevant to salient stimuli occurring in any physical form (e.g., pressure waves, air-particle displacement, chemical, etc.).

Following our general overview of spatial aspects of neural circuitry, we next highlight two examples—one focused on target selection and one focused on action selection—to further elucidate spatial aspects of target and action selection in behaviorally relevant contexts.

Spatial attention—an example of target selection in the vertebrate midbrain

We use this section to describe some of the conserved neural substrates implicated in spatial attention in vertebrate systems to illustrate general principles of lateral inhibition and recursive connections. Similar principles are implicated in the features of selective spatial attention present in insects (de Bivort and van Swinderen 2016; Nityananda 2016). In vertebrates, neural correlates of selective spatial attention emerge in both the midbrain and forebrain. We highlight in particular the tectum (also called optic tectum, or superior colliculus in mammals) in the midbrain as a key contributor to selective spatial attention (Knudsen 2011; Lai et al. 2011). A subset of the tectum in most vertebrates includes a topographic visual map of space, in which adjacent neurons respond to visual stimuli from adjacent parts of the external world (Knudsen 2011; Hoffmann et al. 2016). Visual stimuli within the part of the visual field to which the animal is directing

its attention evoke higher activity and different temporal rhythms in tectal neurons (e.g., Winkowski and Knudsen 2007). Another distinct subset of tectal neurons encodes an orientation map of space that directs the gaze or head position toward a specific part of the world, or modulates covert attention (orienting without moving the body) (Knudsen 2011). These two maps—the topographic and orientation—are closely linked in many species. Salient visual stimuli activate orientation-related tectal neurons to rapidly direct movements that place the stimulus in the animal's fovea (e.g., Klier et al. 2001), demonstrating a direct interaction between target and action selection. Additionally, the orientation map typically receives inputs from other sensory modalities that are all in spatial register (Stein et al. 1975; Harris et al. 1980; Bastian 1982; Knudsen 1982; Triplett et al. 2012). The tectum thus coordinates orientation responses to visual, auditory, or electrosensory stimuli depending on the species' sensory specializations (reviewed in Barron and Klein 2016). For example, tectal orientation neurons in bats that navigate using echolocation signals will direct sonar in space in response to auditory (as opposed to the more typical visual) signals (Hoffmann et al. 2016). Orientation-related tectal neurons are strong candidates for mediating selective spatial attention, as their activity levels appear switch-like, with sudden shifts between high and low action potential firing rates as the 'top-priority' stimulus changes (Knudsen 2011; Lai et al. 2011).

Given that topographic and orientation maps facilitate the activation of neurons dedicated to certain areas of physical space, how does the tectal circuitry select a particular space as target of attention? This process is influenced by both stimulus-driven (bottom-up) and contextual (top-down) processes (reviewed in Knudsen 2011; Lai et al. 2011). The stimulus-driven processes that mediate spatial attention involve (i) projections from neurons in the nearby midbrain isthmal nucleus that amplify responses to stimuli in the target part of space and (ii) projections from a separate population of isthmal neurons that inhibit responses to stimuli in nontarget parts of space (Wang 2003; Marín et al. 2005, 2007; Gruberg et al. 2006; Mysore and Knudsen 2013) (**Fig. 2**). This (i) local enhancement and (ii) lateral inhibition allow the animal to maintain attention in one part of the world. However, target switching can occur either when the animal habituates to ongoing stimuli or when particularly salient stimuli (e.g., rapidly approaching stimuli that could represent predators) induce very large

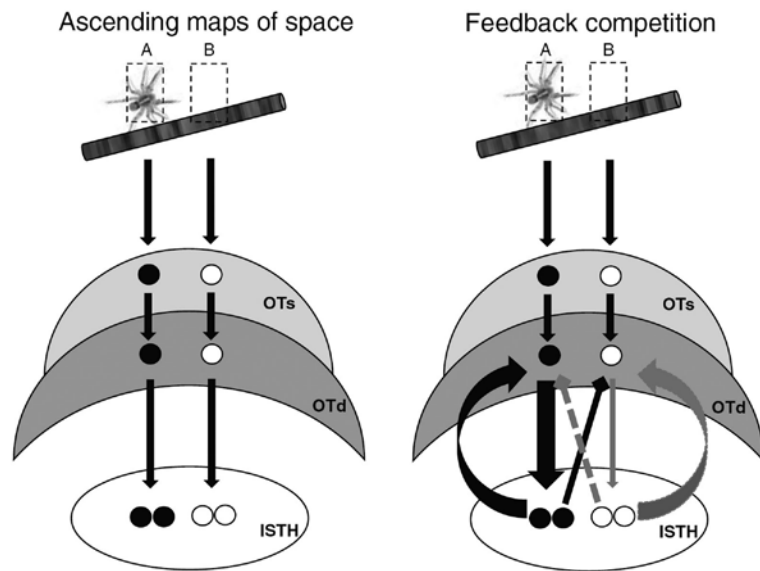


Fig. 2. Heuristic diagram of a vertebrate tectal circuit that implements a form of target selection implicated in selective spatial attention. Visual stimuli from spatial locations A (black circles) and B (white circles) are shown mapped onto layers of the optic tectum. The superficial layers of the optic tectum (OTs) contain a sensory map of space, which in most species is a predominant input into the multi-sensory orientation map in the deep layers of the optic tectum (OTd). Tectal information is passed to the isthmal nuclei (ISTH). The right panel demonstrates that visual stimulation from point A leads to local enhancement of tectal responses to stimuli from location A via excitatory feedback projections from a set of isthmal neurons (signified by the black curved arrows on the right panel). Moreover, feedback inhibition from a different set of isthmal neurons corresponding to spatial location A suppresses tectal neurons corresponding to other locations in space (indicated by the black line ending with diamonds). Stimulation from point B activates the same two feedback loops (indicated by the gray arrow and dashed gray line), but this example posits that this feedback is weaker because the spider at position A is a more salient stimulus than the visual stimulus at location B, thus attention is directed toward location A.

sensory responses that rapidly override the previously attended target via lateral inhibition (Lai et al. 2011; Dutta and Gutfreund 2014).

The tight link between tectal sensory maps and orientation maps allows researchers to use an animal's gaze or orientation as a behavioral readout of spatial attention that complements neurophysiological information. Rapid advances in wearable technology (e.g., eye-trackers and miniature cameras) have made it possible to explore the details of selective spatial attention and target-switching in free-living

animals. For example, such technologies have revealed new information about how peahens visually switch between scanning the environment and assessing particular traits of potential mates (e.g., Yorzinski et al. 2013, 2015). As we begin to integrate such details of selective spatial attention in free-living animals with neural circuit dynamics, we will likely gain greater insights into the principles by which sensory systems dictate animal communication in particular. For example, certain types of dynamic movements or elaborate morphology might help capture an animal's focus on a particular receiver or might help maintain attention throughout an ongoing display by overcoming habituation. Attentional processes might work differently when assessing novel individuals rather than familiar individuals or displays. Therefore, processes underlying selective spatial attention have the potential to shape the evolution of signal form.

In addition to external stimulus-driven processes as just outlined, target selection is also modulated by internal contextual processes—by feedback from forebrain areas that bias the competition among possibly salient stimuli in the midbrain–isthmal circuit (Lai et al. 2011; Mysore and Knudsen 2014). Anatomical inputs from many forebrain regions reach the tectum and other sensory processing centers and could bias target selection based on previously learned associations or current physiological needs (Mysore and Knudsen 2014). For example, when animals are reproductively active, circulating hormones and neuromodulatory inputs from the forebrain may bias the competition in favor of environmental stimuli that reflect potential mates. Although relevant neuromodulatory inputs and hormone receptors exist in the tectum, we have little information currently about how forebrain pathways adjust tectal sensory processing to match physiology or context. As one possible example in which tectal processing depends on context, the neuropeptide GnRH3 suppresses responses of the tectum to retinal inputs in a fish, and hence may contribute to differences in sensory processing based on reproductive condition (Umatani et al. 2015). These contextual processes of target selection will be the key to understanding how behavioral responses to the same stimulus may change across seasons or with experience.

In sum, tectum–isthmal circuits in vertebrates mediate a form of sensory gating in which the most relevant sensory signals are relayed to forebrain and motor circuits, while irrelevant or stable stimuli are

filtered out or suppressed. The neural circuit connections, including lateral inhibition within feedback and feedforward loops, dynamically enhance responses to target stimuli and suppress responses to competing stimuli. These hierarchical networks enable context-dependent shifts in which parts of the external world gain access to sensory processing resources and weigh most heavily in upcoming behavioral outputs. We propose that the means by which stimuli capture and maintain selective spatial attention contribute to diverse behavioral outcomes, including preferences for signals with particular dynamic movements and contrast patterns as well as the dependence of behavioral responses on physiology, current environmental context, and previous experience.

Goal-directed locomotion: an example of action selection in the insect central complex

In addition to processing stimuli from specific locations in the environment, animals also produce cohesive, coordinated behavioral responses to spatially explicit external stimuli, even in the face of multiple competing (and potentially conflicting) sensory cues. Here, we discuss how action selection processes produce such cohesive behaviors. To do this, we use a well characterized example of goal-oriented locomotion in insects.

Goal-directed locomotion is a major component of many behaviors: foraging involves navigating toward likely food resources; migration involves long-distance, goal-directed movement; aggressive or reproductive behavior often starts by approaching a conspecific; and avoiding predators or competitors requires locomotion away from a risky location. Accurate locomotion requires neural representations of (1) the location of a target for approach or avoidance, often including short term memory that maintains that target when immediate sensory cues are lacking; (2) the organism's current position relative to the target; and (3) corrective motor commands that adjust the current heading to avoid obstacles and reach the intended destination. In insects, part of the brain called the central complex coordinates these functions to implement goal-directed locomotion, while diverse sensory cues might indicate the locations of possible navigation targets.

Sensory inputs related to a navigation goal reach neurons in the central complex, where sensory information retains a spatial component (**Fig. 3**). For example, visual neurons in the protocerebrum encode landmarks or light polarization (Lin et al. 2013; Seelig and Jayaraman 2013; el Jundi et al. 2015; Kakaria and de Bivort 2017). Axons from these sensory interneurons converge on neurons in the ellipsoid body (alternatively termed the lower division of the central body; Lin et al. 2013). Activity in these ellipsoid body neurons corresponds to the animal's orientation relative to its destination (Seelig

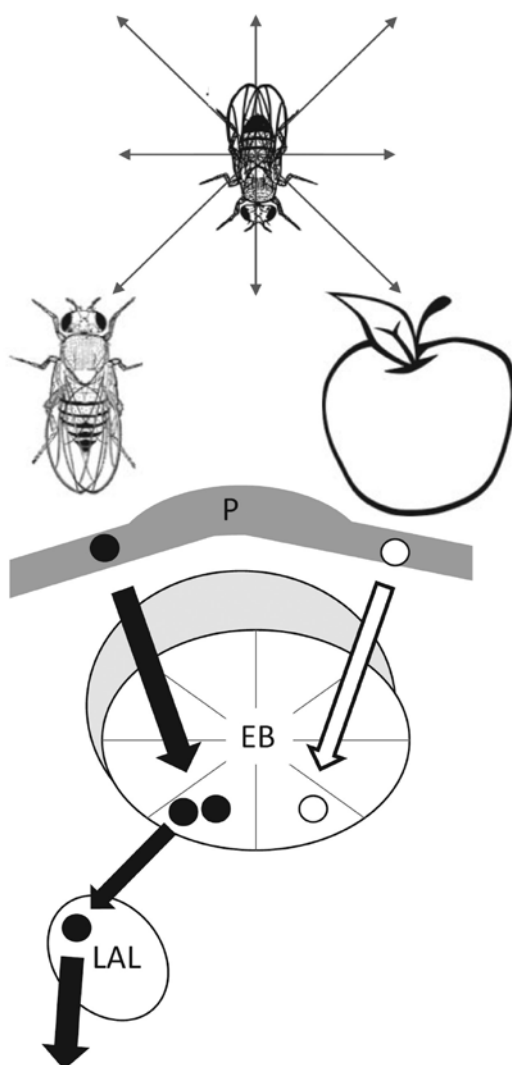


Fig. 3. Goal-directed navigation behaviors in *Drosophila* depend on action selection circuits in the central complex. We depict brain regions as larger shapes, and individual neurons as small circles, with anatomical connections indicated by arrows. Sensory inputs from regions such as the protocerebrum (P) converge on the ellipsoid body (EB), with stimuli from a given range of the world projecting to neurons in a single EB wedge. Possible orientations compete against one another via lateral inhibition (not depicted) such that only one EB wedge is active at a time, representing the animal's current heading in space. EB neurons project to motor areas in the lateral accessory lobe (LAL) to implement the appropriate steering responses. For example, males follow females in flight as part of courtship, and thus would steer toward visual stimuli consistent with female flies. Such a stimulus would outcompete other less salient stimuli as the destination. The salience of flying conspecifics depends on context, however, as male flies escalate to following only with recent exposure to chemicals of receptive females. In most other situations, the parts of the world with small moving stimuli would be less likely to win the competition.

and Jayaraman 2015; Green et al. 2017; Kim et al. 2017; Turner-Evans et al. 2017). In turn, the outputs of these ellipsoid body neurons modify premotor neurons in the lateral accessory lobe. These premotor neurons then project to motor patterning neurons that establish locomotor speed and initiate turns in cockroaches and flies (Guo and Ritzmann 2013; Martín-Peña et al. 2014; Martin et al. 2015).

As with spatial attention in the vertebrate midbrain, the functioning of the insect central complex navigation circuit depends on competition among possible destinations via reciprocal inhibitory connections. Computational models demonstrate that the connectivity pattern among neurons in the network promote a winner-take-all property by which one destination emerges, even across a wide range of synaptic connection strengths (Kakaria and de Bivort 2017; Kim et al. 2017). The ellipsoid body integrates diverse noisy sensory inputs in a way that enables prioritization across sensory modalities (Kottler et al. 2017). Computational models recapitulate key electrophysiological findings from ellipsoid body neurons in flies (Seelig and Jayaraman 2015) and cockroaches (Varga and Ritzmann 2016): ongoing neural activity represents the chosen destination even when sensory cues are not available (for at least 30 s) and switch-like changes can shift the destination (Kakaria and de Bivort 2017). This switch-like activation and continuity across time is required for the coordination of a series of actions that comprise one goal, such as avoidance of a predator or approaching a prey item (Kottler et al. 2017). Similar to the spatial attention circuitry discussed previously, the winner-take-all nature and circuit stability of goal-directed locomotion, on the time scale of tens of seconds, are consequences of lateral inhibition and recurrent projections (Kakaria and de Bivort 2017; Kim et al. 2017; Kottler et al. 2017).

In addition to goal-directed locomotion, central complex neurons are also implicated in reproductive and aggressive behavior, suggesting that competitive interactions within this circuitry might contribute to action selection among broader categories of behavior (e.g., goal-directed locomotion, attacks, and vocalizations) (Kottler et al. 2017). Understanding how neural circuit dynamics contribute to both persistence in executing a series of behaviors and switch-like changes may help behaviorists explain observed patterns of behavior such as attack versus mate in sexually cannibalistic species (Hebets 2003). Similarly, investigating mechanisms of observed variation within and across species in assessment time before initiating responses to potential mates

or adversaries could provide fundamental insights into both context-specific behavior and to neural mechanisms by which a selected action is initiated.

Studies exploring the proximate basis of goal-oriented locomotion are beginning to elucidate the mechanisms of divergence of reproductive behaviors across taxa. For example, conspecific vocalizations elicit receptive females to decrease flight speed to allow mating in fruit flies, whereas they direct female phonotaxis in crickets. The auditory neurons that process these vocalizations likely interact with the central complex navigation circuit to bias behavior differently in each species, and do so in a manner that depends on sex and reproductive state. In *Drosophila melanogaster*, antennal mechanosensory neurons project into neurons in the protocerebrum that are tuned to parameters of conspecific song (Vaughan et al. 2014). These neurons in turn project to female-specific clusters that also respond to pheromonal stimuli (Zhou et al. 2014) and are implicated in slowing flight speed of receptive females (Coen and Murthy 2016). In crickets, auditory neurons in the protocerebrum respond to conspecific calls and direct steering responses via interneurons that directly contact the premotor lateral accessory lobe neurons (Zorovic and Hedwig 2011). In crickets then, each sound pulse triggers corrective steering in receptive females engaged in phonotaxis. As the neural mechanisms mediating slowing or phonotaxis behavior are described more comprehensively, we will begin to understand how divergence in the protocerebrum-ellipsoid body-lateral accessory lobe circuitry might regulate diversity in reproductive behaviors across lineages.

In summary, research in the insect central complex highlights that producing a single coherent action involves widespread suppression of alternative actions and a mechanism that facilitates a winner-take-all property of action selection (Kottler et al. 2017). A very similar balance of inhibition and excitation underlie action selection in the basal ganglia of vertebrates, which recently was argued to be homologous to the insect central complex (Strausfeld and Hirth 2013; Fiore et al. 2015). Neuroanatomy, modeling, and physiology in basal ganglia and central complex circuits also reveal clearly that target selection and action selection can occur simultaneously. Importantly, target selection in sensory areas does not necessarily precede action selection, but rather the hierarchical circuits implementing each process interact (Cisek 2007; Fiore et al. 2015). For example, a display element that captures an animal's attention will cause it to orient or direct its

attention toward the sender, which will influence the later sensory inputs the animal receives, hence biasing it toward particular actions. The interaction between target and action selection is imperative to keep in mind when trying to study animal behavior, as the ‘decision’ that scientists read out often emerges from a progression of assessment-related behaviors that may be interdependent and may each have distinct sensory or cognitive biases.

Temporal aspects of target and action selection

Target selection and action selection circuits must not only integrate sensory inputs across distinct physical forms (e.g., sensory modalities) in space, but also in time. Animals may accumulate information over long time scales (e.g., over a lifetime) or short time scales (within a single display or cue). Sensory neurons respond to very brief stimuli in the millisecond time scale, and thus even assessment of an individual call or display element typically involves integrating a series of individual stimuli. Longer term assessments of displays require grouping a series of individual stimuli as arising from a single sender. Such temporal dynamics are critical for understanding how animals integrate complex information such as social signals.

Bimodal neurons respond to concurrent stimuli that excite receptors from different sensory systems (e.g., visual and acoustic). Such bimodal neurons often function in a manner such that either sensory input—e.g., visual or acoustic—can depolarize the neuron, with bimodal cues (e.g., visual–acoustic) generating additive or supra-additive effects via summation of sensory inputs (reviewed in Stein 2012). Numerous nonlinear combinations, however, are also possible. For example, complex receptive fields exist in which the firing rate of the postsynaptic neuron depends not only on simultaneous stimulation of multiple sensory receptors (e.g., multiple hair cells excited at different frequencies) but also on a temporal sequence of signal elements. It is well established that responses of sensory neurons can depend on temporal patterning of the stimulus, as evidenced by neurons in which only stimuli of certain durations, speed, or frequencies elicit action potentials (reviewed in David and Shamma 2013). The details of the summation across sensory inputs over time establish the multisensory neuron’s tolerance to the range of combinations of sensory elements.

The sensitivity of neural activity to temporal patterning in stimuli likely contributes to mate choice preferences for trill properties in some bird species (Ballentine et al. 2004; de Kort et al. 2009) and pulse timing properties in some frog species (e.g., Gerhardt and Schul 1999; Lemon 2009). Neural responses to the same stimulus element (e.g., one syllable or one stereotyped motion) can depend on how that element fits within a dynamic display (reviewed in Eggermont 2011). Importantly, temporal integration in neural circuitry over different time scales can be influenced by multiple mechanisms, including short term plasticity within the presynaptic neuron, temporal summation in the postsynaptic neuron, as well as dynamic properties of the whole interconnected network of neurons (reviewed in Buonomano and Maass 2009; Goel and Buonomano 2014). We introduce each in turn and discuss broad network consequences of this temporal integration.

Short term plasticity—short-term synaptic plasticity is one means by which recent history of high firing rates can either enhance (i.e., facilitate) or reduce (i.e., depress) responses to subsequent inputs. The effects of short term synaptic plasticity tend to last hundreds of milliseconds (reviewed in David and Shamma 2013). For example, short-term synaptic facilitation occurs when rapid firing rates lead to calcium build-up in the presynaptic neuron. This elevated calcium level increases the amount of neurotransmitter released to later elements (e.g., notes or movements) of a stimulus stream (e.g., a song or visual display) and thereby enhances postsynaptic responses to later stimulus elements in a series. In contrast, short-term synaptic depression occurs when the pool of releasable neurotransmitter vesicles has been depleted as a consequence of extensive firing. Short-term synaptic depression is implicated in a common property of sensory neurons, stimulus-specific adaptation, in which repeated presentation of a given stimulus evokes reduced responses in neurons that would respond vigorously to a novel stimulus (Ulanovsky et al. 2003; Ulanovsky 2004; May et al. 2015). Stimulus-specific adaptation has been extensively studied at multiple stages of processing in vertebrate auditory systems (e.g., Antunes and Malmierca 2011; Malmierca et al. 2015) and is a common phenomenon present in diverse sensory systems.

Temporal summation—a series of action potentials in presynaptic neurons will cause temporal summation in the postsynaptic neuron. Diverse ion channels participate in postsynaptic voltage changes even for subthreshold responses that do not initiate action potentials, such that membrane voltage diverges from the standard resting potential

for tens of milliseconds after presynaptic action potentials (reviewed in David and Shamma 2013). Whether the postsynaptic neuron reaches a threshold for firing an action potential, or a burst of action potentials, will depend on whether the momentary voltage is above, below, or at the resting potential of the neuron. This summation is central in building receptive fields that integrate over tens of milliseconds, such as auditory or electrosensory neurons that count pulse number or intervals between pulses (e.g., Alder and Rose 1998; Edwards et al. 2002; Clemens et al. 2011; Baker and Carlson 2014; Schoneich et al. 2015). These postsynaptic summation mechanisms can also integrate over different inputs at several time periods to build complex combination-sensitive receptive fields (e.g., Sadagopan and Wang 2009; Aubie et al. 2012). In such neurons, two or more channels may be necessary to induce responses, or one channel might suppress a response to a second. Thus, even at early stages of sensory processing, complex receptive field properties can reflect behaviorally relevant stimulus combinations over short time scales.

Dynamic network properties—temporal integration also arises from diverse network-level properties (reviewed in Goel and Buonomano 2014). Dynamic patterns of action potential firing in the numerous neurons that comprise a neural circuit can be considered the network state of the circuit (Buonomano and Maass 2009; Miller 2016). Recent patterns of circuit activity bias the current network state and likely future states (e.g., Morcos and Harvey 2016). One way computational neuroscientists conceptualize and model dynamic patterns is as discrete network states, termed ‘attractors’, toward which circuit dynamics automatically drift due to intrinsic properties of the circuit (e.g., anatomical and physiological details of synapses; reviewed in Miller 2016). The network state could switch between attractors when novel sensory responses perturb activity in the network such that dynamics drift to another discrete network state. Other modeling approaches focus on long-range oscillations over diverse time scales as a means to describe network dynamics (Miller 2016). Each circuit has intrinsic time scales over which recent activity modifies the probabilities of future alternative network trajectories, and these effects can last tens of seconds or longer (Buonomano and Maass 2009; David and Shamma 2013; Goel and Buonomano 2014). These circuit-level dynamics shape the neurophysiological responses of single sensory neurons to complex sensory stimuli. For example, findings that neural responses to individual display elements do not predict responses to

those elements as part of complex displays are common (e.g., Theunissen et al. 2000; Beetz et al. 2016). Top-down network connections likely sculpt the responses to a single element based on the broader display context over time ranges that can span seconds.

The influence of recent stimulus history on network dynamics can yield phenomena such as predictive temporal processing, in which neural circuit feedback loops generate predictions or expectations of upcoming stimulus elements. For example, neurophysiological responses in the rat auditory cortex are reduced by stimulus repetition within a few minutes even for a series of 20 tones spanning several seconds; the same neurons, however, respond vigorously when a tone in that series is modified from the ‘learned’ order (Yaron et al. 2012). This suggests that neuronal response is not simply modulated by stimulus-specific adaptation mechanisms. Rather, top-down inputs generate an expected tone sequence and neural firing is reduced only when the expectations are met, whereas unexpected stimuli, such as a tone occurring out of sequence, induces vigorous responses in the nervous system. Reduced firing to a broad range of expected stimuli is likely to be metabolically efficient by decreasing the computational resources dedicated to ‘known’ features of stimuli (e.g., Winkler et al. 2012), and may also play a role in neural responses to learned stimuli if these network-level changes persist over longer time scales. Sensory systems generally have a biased representation of the world that integrates across time scales to generate expectations of which stimulus features are most salient for behavioral decisions.

Together, features of short-term plasticity, intrinsic integration in neurons, and network-wide phenomena determine how recent stimulus history (over milliseconds, seconds, and even minutes) sculpts sensory responses to ongoing stimuli. These network dynamics emerge from common circuit motifs such as feedforward and feedback loops, and can occur with or without an explicit mechanism of learning and memory, in which experience-dependent changes in network function persist over longer time scales. We propose that the intrinsic dynamics of these neural circuits shape stimulus features by creating complex sensory biases. For example, dynamic displays might create greater sensory responses if they overcome stimulus-specific adaptation and predictive coding. We might thus expect greater neural responses and behavioral preferences for novel, less repetitive displays. Preference for novelty or complexity is common in songbirds, and measurements of complexity that capture these neural response dynamics might better

identify preferences for complex signals that evoke enhanced neural activity. Understanding the basic neural firing properties can thus help distinguish preferences due to sensory or perceptual biases from those preferences that more likely evolved in receivers.

Conclusions

Neural circuit architecture and dynamics enable target and action selection, which underlie all animal behavior. When animals are reacting to stimuli in the external world, neural circuit activity can reflect the source of stimuli in physical space and can integrate inputs from different sensory systems over time. Moreover, multiple mechanisms mediate temporal integration of stimuli on different time scales, from less than a second to a lifetime. Given this underlying complexity, variation in stimulus preferences and/or behavioral strategies could reflect many distinct mechanistic changes in neural circuitry.

Conceptualizing animal behavior as the result of shifting states in a dynamic neural circuit accommodates the classical view of sensory-motor integration, but offers much more potential for nonlinearity that better matches the observed complexities in behavior. Throughout this paper, we have highlighted how dynamic networks can explain behavioral outputs, as network dynamics in target selection and action selection circuits shift between modes depending on sensory inputs. The spatial and temporal patterns inherent in neural processing create inherent biases in animals for particular details of complex displays. Moreover, certain forms of context-dependent behavior may emerge naturally from network state dynamics rather than reflecting selection for adaptive context dependence. These spatio-temporal properties also shape the energetic demands of particular sensory decisions, as discriminations that depend on natural neural circuit dynamics may allow more efficient neural computations that impose lower metabolic demands than other types of discriminations. The spatial and temporal elements of target and action selection circuits may thus redirect researchers toward deeper consideration of behavioral and neural details in order to develop a more comprehensive and accurate understanding of the factors shaping behavioral diversity. Such integrative work will also likely elucidate the interaction between higher cognitive processes and neural circuitry dynamics in producing complex sensory-guided behavior.

Acknowledgments — The authors thank three anonymous reviewers for their helpful comments on this manuscript.

Funding — This work was supported by the Hanse-Wissenschaftskolleg [to K.L.H.].

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