

Integration of parallel mechanosensory and visual pathways resolved through sensory conflict

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Edited by William Bialek, Princeton University, Princeton, NJ, and approved September 8, 2016 (received for review November 28, 2015)

The acquisition of information from parallel sensory pathways is a hallmark of coordinated movement in animals. Insect flight, for example, relies on both mechanosensory and visual pathways. Our challenge is to disentangle the relative contribution of each modality to the control of behavior. Toward this end, we show an experimental and analytical framework leveraging sensory conflict, a means for independently exciting and modeling separate sensory pathways within a multisensory behavior. As a model, we examine the hovering flower-feeding behavior in the hawkmoth *Manduca sexta*. In the laboratory, moths feed from a robotically actuated two-part artificial flower that allows independent presentation of visual and mechanosensory cues. Freely flying moths track lateral flower motion stimuli in an assay spanning both coupled motion, in which visual and mechanosensory cues follow the same motion trajectory, and sensory conflict, in which the two sensory modalities encode different motion stimuli. Applying a frequency-domain system identification analysis, we find that the tracking behavior is, in fact, multisensory and arises from a linear summation of visual and mechanosensory pathways. The response dynamics are highly preserved across individuals, providing a model for predicting the response to novel multimodal stimuli. Surprisingly, we find that each pathway in and of itself is sufficient for driving tracking behavior. When multiple sensory pathways elicit strong behavioral responses, this parallel architecture furnishes robustness via redundancy.

sensory integration | redundancy | animal locomotion | control theory | system identification

Animals rely on a convergence of information across parallel sensory pathways to control locomotion. In these neural control strategies, one sensory modality may contribute concurrently to several behaviors (a one-to-many mapping), and conversely, several sensory modalities may collectively govern a single behavior (a many-to-one mapping). A continuing aim in studies of animal behavior is to extricate the contribution of an individual sensory modality from the ensemble of pathways (that is, the one-to-one mapping from a sensory percept to the locomotor action; e.g., the optomotor response, chemotaxis, vestibular postural reflex, etc.). The dynamics of locomotor behaviors, however, are shaped by the combination of and interactions between sensorimotor pathways. Therein remains a fundamental challenge in understanding multisensory integration: how does the nervous system combine these streams of information to control behavior, and how do we separate the relative contributions of sensory pathways in the context of a parallel topology?

There is no single answer. Across taxa and behaviors, nervous systems instantiate varied policies for integrating sensory information across modalities. In many instances, parallel sensory pathways serve complementary roles. For example, when humans perform reaching tasks, the planning of motion trajectories relies heavily on visual information, whereas the control of arm movements favors proprioceptive cues (1). In flies, the visual and haltere mechanosensory systems are sensitive to slower and faster rotational motions, respectively, extending the behavioral response to a broader range of motion by this separation of sensory sensitivities (2). In contrast, this work explores a behavior in

which parallel sensory pathways contribute to the same task concurrently and over the same frequency spectrum.

The nectivorous hawkmoth, *Manduca sexta*, feeds via a long proboscis while hovering in front of a flower, continually modulating flight to maintain a frontal position as the flower sways. This flower-tracking behavior has become an experimental paradigm for the study of visuomotor responses (3, 4). However, the proboscis is covered with mechanosensory sensilla, and specifically, the basal sensilla of pilifer are thought to encode the deflection of the proboscis with respect to the head (5).

The relative contributions of sensory pathways are commonly tested by means of sensory isolation (e.g., isolating mechanosensory pathways by ablating or painting the eyes, inhibiting the visual pathway, or eliminating visual cues). However, this approach would fail to reveal particular neural control strategies. In redundant neural control systems, inhibiting a single pathway manifests little change in performance. Moreover, animals may adapt to such manipulations; recent studies of this flower-tracking behavior have illuminated mechanisms that compensate for reduced light (4). Thus, sensory isolation may not be informative of the sensory dynamics under natural conditions, when a suite of senses participate. Instead, we present conflicting visual and mechanosensory stimuli to dissociate the two modalities while maintaining the sensory pathways intact—similar to human psychophysical experiments in reaching (1) and posture control (6) and experiments in joint visual-electrosensory tracking behaviors in knifefish (7).

Flying insects rely on a concert of sensory inputs to control flight, but the sufficiency and necessity of the visual system often overshadow the contribution of other sensory pathways. Indeed, mechanosensory organs serve key roles in insect flight control: antennae (8–11), halteres (2, 12), or wings (13). Prior studies

Significance

Animals rely on information drawn from a host of sensory systems to control their movement as they navigate in and interact with their environment. How the nervous system consolidates and processes these channels of information to govern locomotion is a challenging reverse engineering problem. To address this issue, we asked how a hawkmoth feeding from a moving flower combines visual and mechanical (force) cues to follow the flower motion. Using experimental and theoretical approaches, we discover that the brain performs a remarkably simple summation of information from visual and mechanosensory pathways. Moreover, we reveal that the moth could perform the behavior with either visual or mechanical information alone, and this redundancy provides a robust strategy for movement control.

Author contributions: E.R., T.L.D., and S.S. designed research; R.W.H. and S.S. performed research; E.R. and S.S. analyzed data; and E.R., T.L.D., and S.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1522419113/-DCSupplemental.

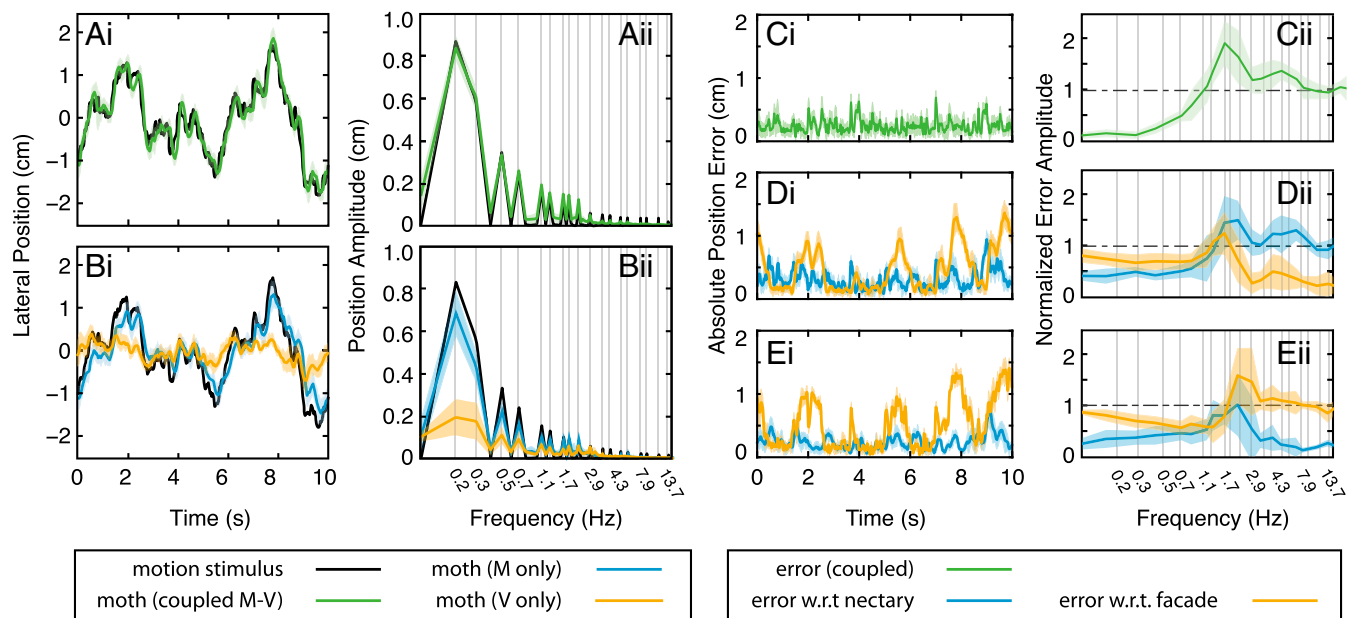


Fig. 2. Tracking performance of moths following fictive flowers under three motion stimulus conditions: (A) the flower face and nectary move through identical trajectories, $r_m(t) = r_v(t)$ (green; the coupled condition; mean and 95% confidence; $n = 8$), (B) the nectary oscillates while the flower face is stationary, $r_v(t) = 0$ (blue; the M-only condition; $n = 8$), and the nectary is stationary, $r_m = 0$ (gold; the V-only condition; $n = 8$), while the flower face oscillates. (A, *i* and B, *i*) Time traces of tracking trials show slightly degraded tracking in response to only nectary motion and severely impaired tracking when the flower face provides the motion stimulus. (A, *ii* and B, *ii*) The magnitude of the Fourier transform of the moth's trajectory compared with the motion stimulus reveals that, for all conditions, the moth attends to the moving target; the spectra of moth positions show spikes in power at those frequencies that compose the input motion stimulus. (C, *i*) For the coupled condition, the visual and mechanosensory slips (green) are equivalent and therefore, can be simultaneously minimized. (D and E) For the M- and V-only conditions, respectively, the errors $e_v(t)$ (gold) and $e_m(t)$ (blue) reflect a balance of competing sensory pathways. The similarity in error signals between the two conflict conditions is notable considering the categorical differences in stimulus presentation and moth response. w.r.t., with respect to.

weights are unchanged as a function of the stimulus motion content. It is important to note that, unlike assays that test sensory weighting as a function of reliability, the agreement (or lack thereof) between the motion stimuli does not affect the signal-to-noise ratio of either sensory pathway.

Remarkably, the time courses of the error signals are quite similar in the M- and V-only conditions (Fig. 2D and E), despite the dramatic differences in moth flight trajectories in these experiments. For the coupled condition, nectary and flower face move coherently, giving a single error signal $e_m(t) = e_v(t)$ (Fig. 2C). For the M- and V-only conditions (Fig. 2D and E, respectively), we compare the mechanosensory (blue in Fig. 2D and E) and visual errors (gold in Fig. 2D and E). In the M-only condition, the moths' trajectories closely follow the mechanical stimulus (the moving nectary), resulting in a greater visual slip. In the V-only case, the trajectory of the moths' lateral motion is substantially attenuated, again yielding close tracking of the now stationary nectary. The resulting error is nearly identical to that from the M-only condition, favoring lower mechanosensory error at the expense of increased visual slip. Comparing M- and V-only conditions in the frequency-domain representation of error (Fig. 2D, *ii* and E, *ii*), the behavior favors lower mechanosensory error at the expense of increased visual slip at the lower behaviorally relevant frequencies; at high frequencies, tracking performance attenuates (for all conditions), and as a result, the errors converge to a baseline, in which slip with respect to the moving stimulus nears unity and error with respect to the motionless stimulus approaches zero (Fig. S1).

In sensory conflict, it is not the case that moths are worse at tracking the motion stimulus for lack of sensory information. Rather, the observed attenuation is the response to the motion stimulus mitigated by a response to the stationary stimulus. Surprisingly, the mechanosensory pathway is more heavily weighted than the visual.

Mechanosensory and Visual Contributions Sum Linearly. The control strategy that underlies this behavior balances (with some unequal weighting) the perceived visual and mechanosensory slips, and this strategy is consistent across the conflict paradigms tested. How are these signals consolidated in the coupled condition? A simple hypothesis—and one that has been proposed for the interaction of visual and antennal pathways (9, 10)—is linear summation, and the sensory conflict paradigm is ideally suited for testing this hypothesis.

The frequency-domain approach leverages a convenient property of linear dynamical systems: when excited by a sinusoidal input, the output of a linear dynamical system is a sinusoid at the same frequency, consistently scaled in amplitude and shifted in time by frequency-dependent gain and phase, respectively (Fig. 3). This frequency-preserving property is evinced by the alignment of peaks between the input and output frequency spectra (Fig. 2A and B). A linear dynamical system is described by its transfer function, represented graphically as a Bode plot of the frequency-dependent gains and phases. Behavioral transfer functions are estimated empirically as the ratio of the Fourier transforms of the sampled output (moth motion) and input signal (flower motion), $H(\omega) = Y(\omega)/R(\omega)$, where ω is the frequency variable (Fig. 3 and Fig. S1).

Moths exhibit slight attenuation and phase lag in the M-only stimulus condition (Fig. 3A, blue). In the V-only condition (Fig. 3A, gold), the mean gain is severely attenuated, even at the lowest frequencies (between 0.23 and 0.43 in the range 0.2–1 Hz), and phase is leading in this band. When presented coherent visual and mechanosensory cues (Fig. 3B, green), moths track with high fidelity at low frequencies characterized by near-unity gain and small phase lags.

The block diagram depicted in Fig. 1B suggests a deconstruction of these transfer functions into constituent dynamical blocks.

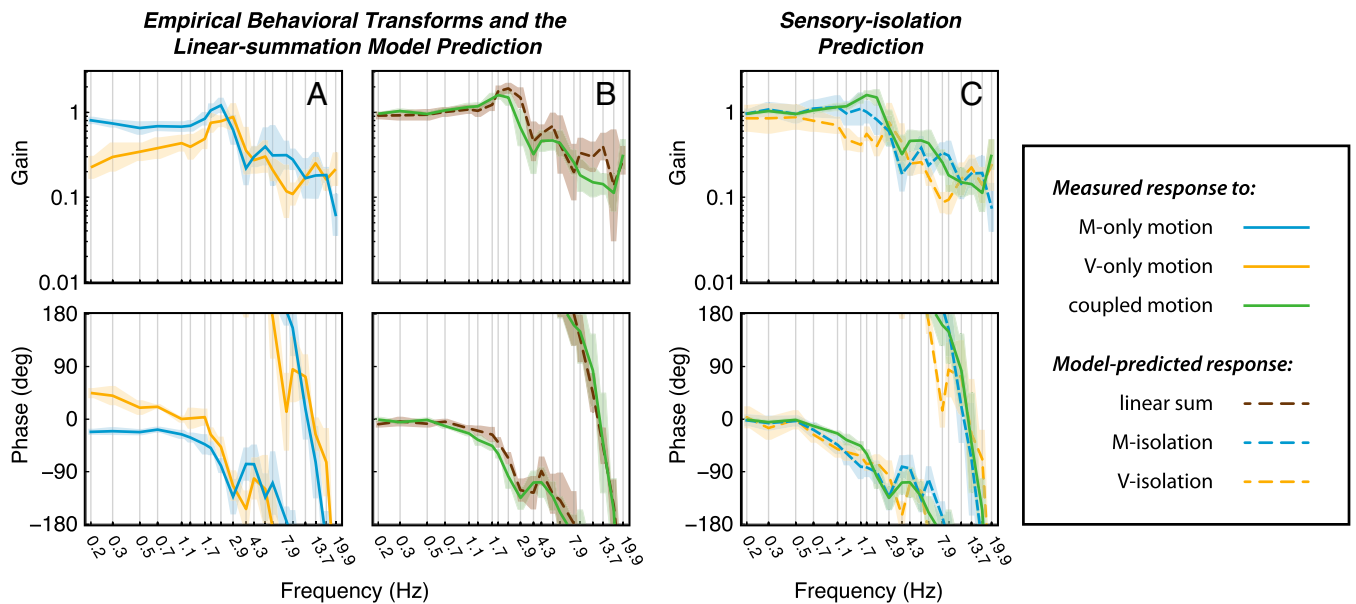


Fig. 3. Bode plots represent graphically the transfer function in terms of two quantities, gain and phase, both as a function of frequency. (*Upper*) Gain is defined as the relative amplitude of the output with respect to the input for the specified frequency component, $|H(\omega)|$; (*Lower*) phase is the relative timing of the output and input signals, $\angle H(\omega)$. Hence, perfect tracking would correspond to unity gain and zero phase (i.e., moth and flower motions are at the same amplitude and synchronized). For a multiinput, single-output system, the transfer function relating the output to an input describes the system response assuming that all other inputs are zero just as we have done experimentally. (*A*) Over the behaviorally relevant frequency band, 0–1.7 Hz (4), the response in the M-only condition (blue; mean and 95% confidence) is characterized by slight attenuation in gain and increased phase lag. In the V-only condition (gold), gain is severely attenuated, even at the lowest frequencies, but phase is leading. (*B*) In response to flowerer motion with coherent visual and mechanosensory cues, moths track with high fidelity at low frequencies characterized by near-unity gain and small phase lags. The sum of the complex-valued transfer functions is superimposed on the coherent response (brown dashed line). The linear sum of M- and V-only responses qualitatively predicts the measured response to coherent stimuli over the entire frequency range tested. (*C*) Assuming linear summation between sensory pathways, we may predict the behavioral response to hypothetical isolation experiments in which one or the other sensory pathway is inhibited or ablated. These data are presented in [Tables S1](#) and [S2](#).

Coupled motion yields the following behavioral transform (we omit the frequency argument ω for clarity):

$$H = \frac{(S_m + S_v)CP}{1 + (S_m + S_v)CP} \text{ and } Y = HR. \quad [1]$$

Also, for the sensory conflict paradigms, the transfer function for the M- and V-only responses is

$$Y = \underbrace{\frac{S_m CP}{1 + (S_m + S_v)CP}}_{H_m} R_m + \underbrace{\frac{S_v CP}{1 + (S_m + S_v)CP}}_{H_v} R_v. \quad [2]$$

Note that, in conflict conditions, both sensory transforms, S_v and S_m , appear in the denominator; the denominator reflects the reafferent pathway, the negative feedback that represents ego motion with respect to both the moving and stationary features. These behavioral transforms reveal an interaction between sensory pathways in closed loop, and therefore, the M- and V-only responses do not transparently represent the open-loop dynamics of the underlying sensory processes.

Still, linear summation implies that the sum of M- and V-only responses predicts the coupled response, $H = H_m + H_v$ (Eqs. 1 and 2). The close agreement between the sum of the M- and V-only responses (Fig. 3*B*, brown dashed line) and the response to coupled stimuli is consistent with a model in which mechanosensory and visual processing occurs on parallel and independent pathways that sum linearly. Moreover, the sensory weights are constant across our stimulus conditions.

Linear Summation Furnishes a Predictive Model. If the linear summation hypothesis truly reflects the underlying computation, then these transfer functions should provide a predictive model,

allowing us to forecast the response to novel combinations of visual and mechanosensory stimuli.

In a final set of experiments, we simultaneously actuate both the nectary and flower face with dramatically different and particularly crafted trajectories. We design two new sum of sines stimuli, $r_m(t)$ and $r_v(t)$, composed of five frequency components at 0.2, 0.7, 1.3, 1.9, and 2.9 Hz (Fig. 4*A*). Using the empirical transfer functions H_v and H_m , we design the inputs (selecting appropriate amplitude and phase at each frequency from [Tables S1](#) and [S2](#)), such that the predicted visual and mechanosensory contributions are identical in amplitude and perfectly antiphase (Fig. 4*B*). The linear summation model predicts that the combined effect of these trajectories should elicit a zero motion response. However, it would then be impossible to differentiate between this cancellation of responses and no response at all (which might be reasonable to expect from an animal presented such a confounding set of sensory stimuli). Therefore, we select a single frequency (0.7 Hz) at which the outputs sum constructively. Hence, the moth receives largely antagonistic sum of sines stimuli and is predicted to respond with a pure sinusoidal trajectory at the prescribed frequency (Fig. 4*C*).

The spectrum of the moth trajectory clearly shows a peak at the selected frequency and attenuation of all other responses (Fig. 4*D*, *Right*). We repeat this experiment, designing the stimuli such that responses at 1.9 Hz sum constructively (Fig. [S2](#)), and as predicted, we observe a significant peak at the desired frequency and attenuation at all others. Importantly, the stimuli used in these two iterations have identical power spectra; only the relative phases between visual and mechanosensory stimuli are changed. The annihilation of antagonistic stimuli further corroborates the hypothesis that sensory integration attenuates noise; if we presume that noise signals on different sensory pathways are independent,

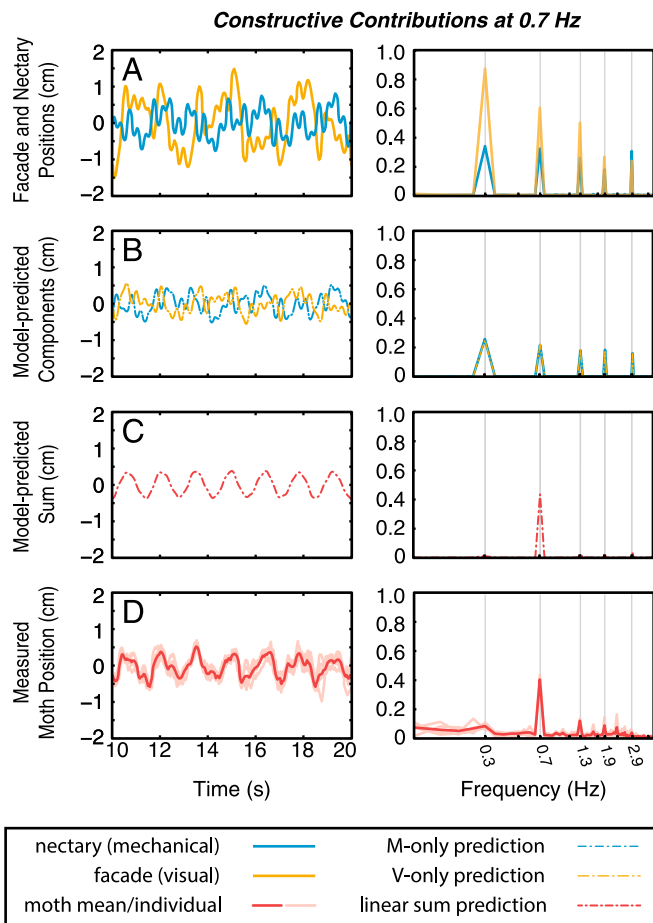


Fig. 4. (A) Specially designed nectary (blue) and flower facade (gold) trajectories should elicit largely destructive motor contributions, in which all frequency components are annihilated except a selected frequency: 0.7 Hz for this case. Note that the amplitude of the visual stimulus is significantly higher to account for the lower gain of the visual pathway in this frequency band. The model predicts (B) the contribution from each sensorimotor pathway (blue and gold dashed lines) as well as (C) their linear summation (red dashed lines). Although we design inputs that would yield a purely sinusoidal moth response, small errors in generating input trajectories result in a slightly imperfect sinusoid prediction. The predicted response represents the empirically measured inputs filtered through the associated behavioral transform functions. (D) Empirical results ($n = 5$) recreate the model prediction. This experiment is repeated with the constructive frequency at 1.9 Hz (Fig. S2).

these components would not combine constructively, yielding reduced noise in the summed output.

The summation model allows us to predictably direct the moths' trajectories. Perhaps most telling, the predictive models that we used to design these trajectories (the M- and V-only Bode plots depicted in Fig. 3A) were each derived from different sets of animals. A third independent group was used to test the predictive model. The population responses predict the individual response, suggesting that the relative gains and phases of responses are highly preserved across individuals.

Mechanosensory and Visual Pathways Provide Redundancy for Control.

“Sensory pathway” refers to the aggregate transformation from error signal to motion output, the cascade of sensory, neural, and physical transforms S_vCP and S_mCP . From these input–output data, it is not possible to further parse the contributions of the constituent blocks. However, we may exploit the commonality between the transfer functions H_m and H_v to calculate the relative gain of the visual and mechanosensory systems, specifically $|S_m|/|S_v| = |H_m|/|H_v|$.

In the decade from 0.2 to 2 Hz, the gain of the mechano-sensory pathway ranges from 3.9 to 1.6 times greater than that of the visual system (Tables S1 and S2). It seems logical that the mechanosensory pathway would carry such weight; the sensory cue is provided by the nectar spur, the actual location of the food source. However, under most natural conditions, the visual cues would be highly correlated to the flower motion as well. In fact, the visual response is not impoverished; rather, it only seems meager when pitted against the more sensitive mechanosensory response.

A statistically optimal sensory summation weights modalities commensurate to their reliability (19). In our experiments, the reliability of each sensory modality is unaffected across presentations, and accordingly, we observe consistent weighting in response to the coupled and conflicting motion stimuli. However, the seemingly feeble visual response raises an important question: for our experiment conditions (lighting, flower geometry, visual background, etc.), are visual percepts deemed unreliable and as a result, attenuated as noise? If so, we should not expect the visual pathway to be sufficient to mediate the behavior on its own in the absence of mechanosensory cues. To the contrary, the visual pathway is independently sufficient. Although this isolation experiment is infeasible, we can estimate the responses of each modality given our existing empirical model.

From the formulations in Eqs. 1 and 2, we could estimate the individual sensorimotor (open-loop) transforms for mechano-sensory and visual pathways G_m and G_v :

$$G_m = S_mCP = \frac{H_m}{1-H} \text{ and } G_v = S_vCP = \frac{H_v}{1-H},$$

where

$$Y = \underbrace{S_mCP}_{G_m} E_m + \underbrace{S_vCP}_{G_v} E_v. \quad [3]$$

Using the estimated sensorimotor transforms, we further construct hypothetical responses for a pair of sensory isolation experiments (Fig. 3C), experiments that we could not perform. Let H'_m be the transfer function describing the feeding response using only mechanosensory cues (e.g., were the moth to feed in complete darkness) (Fig. 3C, blue dashed line). These transfer functions can be represented in terms of empirically measured responses as

$$H'_m = \frac{S_mCP}{1+S_mCP} = \frac{G_m}{1+G_m} = \frac{H_m}{1-H+H_m}. \quad [4]$$

Also, similarly, H'_v would be the isolated visual response (e.g., were we to ablate or inhibit the sensilla on the proboscis) (Fig. 3C, gold dashed line).

For comparison, we replot the mean empirical response from our coupled motion condition (Fig. 3C, green). At low frequencies, the predicted responses are qualitatively similar to the coupled motion condition. Each sensory pathway in isolation seems sufficient to achieve good tracking performance; the pathways are redundant in the context of control.

Discussion

Behavioral Context Shapes Sensory Weighting. In this behavior, the proboscis plays a significant sensory role. However, for a similar task in which moths regulate distance from a looming flower, Farina et al. (16) concluded the opposite: that proboscis-mediated mechanosensory pathways contribute negligibly to the behavioral response. Moths tracking a fictive corolla moving longitudinally along a stationary nectary tube (analogous to our V-only condition) showed only slight attenuation in tracking performance compared with that for an intact flower (analogous to our naturalistic motion

condition). It is likely that the lateral motions that we presented provide a more salient mechanical stimulus than the axial motions associated with looming movements, whereas looming visual motion elicits a strong optomotor response (20). Additionally, Farina et al. (16) conducted experiments on the diurnal moth, *Macroglossus stellatarum*, which may further impact the relative weighting of visual pathways compared with the crepuscular *M. sexta*. Analogously, in the interaction of vision and olfaction, nocturnal moths rely more heavily on olfactory cues, whereas diurnal moths favor visual cues (21). Hence, the weighting between modalities may well depend on the direction of stimulus motion as well as the ecological context to which the moth is adapted.

Sensory Conflict Reveals Redundancy. Although we observe dramatically unequal weighting between visual and mechanosensory transforms, each pathway is in itself sufficient for mediating accurate tracking. Accurate tracking—a behavioral transform $H(\omega)$ near one (Fig. S1)—can be achieved by any sufficiently large sensorimotor transform, $|G(\omega)| \gg 1$ (again, we omit the argument ω):

$$H = \frac{G}{1+G}. \quad [5]$$

Moreover, as the gain of the sensorimotor transform increases, there are diminishing returns in terms of tracking performance, and this insensitivity endows robustness. A behavior arising from parallel sensorimotor transforms, $G_1(\omega)$ and $G_2(\omega)$, and a pair of tunable weighting variables, α_1 and α_2 , is described by the following:

$$Y = \frac{\alpha_1 G_1 + \alpha_2 G_2}{1 + \alpha_1 G_1 + \alpha_2 G_2} R. \quad [6]$$

The above equation represents the behavioral response when both sensory pathways encode the same motion stimulus—the coupled condition. In a sensory isolation paradigm, a single sensory modality is isolated by inhibiting other modalities by either manipulating the animal (e.g., surgical, genetic, or pharmacological) or altering the sensory milieu. In the mathematical representation in Eq. 6, the isolation effectively modulates the weighting variables, α_1 and α_2 . However, if both $G_1(\omega)$ and $G_2(\omega)$

are sufficiently large, the behavioral response is relatively insensitive to modulation of those weights. In nature, this redundancy can confer robustness to damage of a sensory organ or impoverished sensory information that the pathways mutually insure each other. In the laboratory, this robustness presents an experimental challenge in isolating the individual contributions of parallel pathways.

In contrast to isolation, sensory conflict effectively splits the behavioral transform into independently stimulated pathways:

$$Y = \frac{\alpha_1 G_1}{1 + \alpha_1 G_1 + \alpha_2 G_2} R_1 + \frac{\alpha_2 G_2}{1 + \alpha_1 G_1 + \alpha_2 G_2} R_2. \quad [7]$$

Assuming $H(\omega)$ near one, $H_1(\omega)$ and $H_2(\omega)$ are complementary; in conflict, either one or both must exhibit depreciation. For this investigation, we resort to sensory conflict out of necessity (to circumvent the requisite role of vision in insect flight), but the conflict paradigm furnishes a uniquely powerful tool for studying sensory integration.

Conclusion

Through sensory conflict, we show that the flower tracking behavior is mediated by a linear summation of parallel visual and mechanosensory pathways. We do not preclude adaptive sensory reweighting in response to changes in sensory salience or reliability (signal-to-noise ratio). This model provides a general description of the visual–mechanosensory combination that is consistent with previous observations (2, 9, 10) and as such, may represent a more general topology for this sensory integration. More importantly, a single model explains the behavioral responses to both coupled and conflicting motion cues, even when the sensory inputs suggest antagonistic motor outputs. Visual and mechanosensory pathways are, as such, independent, and their summation gives rise to robustness via redundancy.

ACKNOWLEDGMENTS. We thank Eric Warrant and Jeff Riffell for insightful comments on the manuscript. Support was provided by Air Force Research Lab Grant FA8651-13-1-0004; Air Force Office of Scientific Research Grants FA9550-14-1-0398 and FA9550-11-1-0155; The Washington Research Foundation; and the Joan and Richard Komen Endowed Chair (T.L.D.).

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