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Neural basis of sexually dimorphic decision-making

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Animals continually arbitrate between incompatible behaviors: whether to feed or flee, mate or fight, sleep or explore. The brain must select, suppress, and sequence actions according to sensory inputs, internal state, and likely success. Sexual dimorphism adds complexity: males and females face distinct reproductive pressures and often resolve conflicts in divergent ways. Yet the neural mechanisms underlying sex-specific prioritization remain poorly understood. *Drosophila melanogaster* offers a powerful model for dissecting action selection at cellular and circuit resolution. Here, we synthesize recent advances revealing how sexually dimorphic neurons act as integrator hubs, combining sensory cues with internal states to bias choice in both sexes. Neuromodulators confer flexibility, dynamically reweighting priorities as circumstances shift. Dopamine, in particular, filters distracting stimuli and tunes evidence accumulation, enabling priorities to update as goals approach. These studies outline emerging principles of action selection across contexts and sexes and suggest conserved strategies for balancing drives across species.

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Introduction

Animals exist in a perpetual state of decision-making, continuously selecting actions based on shifting internal needs and environmental pressures [1,2]. Conflict arises when competing drives cannot be satisfied simultaneously: whether to feed or flee, sleep or explore, mate or fight. The brain must therefore prioritize; it must select, suppress, and sequence behaviors based on internal needs, external context, and chances of success. This poses a formidable computational challenge: how are competing drives weighted against one another, and how are priorities updated as conditions change?

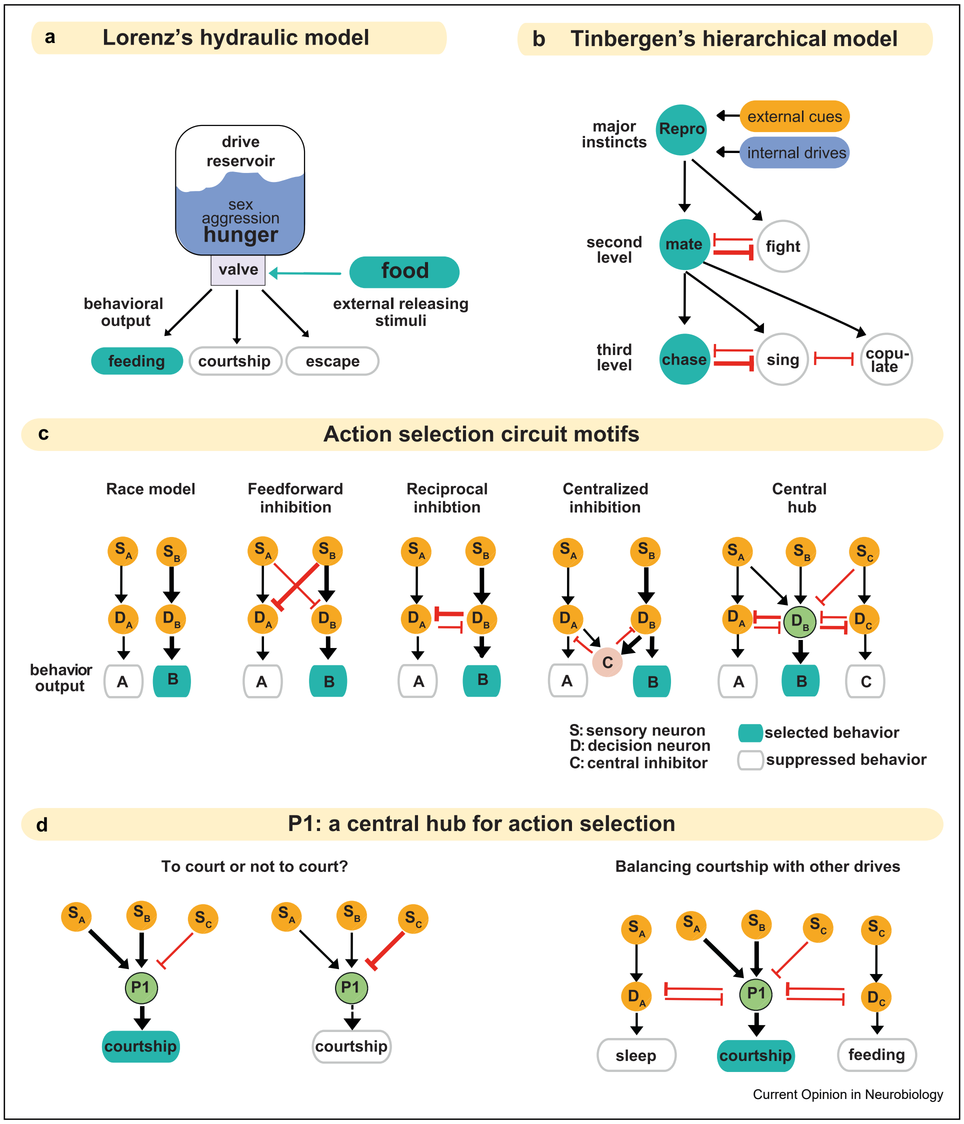
Sexual dimorphism introduces a critical dimension to this challenge. Males and females face distinct reproductive priorities and fitness constraints, which bias how they evaluate risk, reward, and opportunity [3,4]. Males often compete for mates, prioritizing courtship or aggression even at survival's expense. Females incur higher reproductive costs and tend to favor caution, conserving energy or protecting offspring. These evolutionary pressures shape neural circuits and neuromodulatory systems, tuning the thresholds for action selection and biasing how conflicts are resolved.

How then, are behavioral priorities established? Classic ethologists offered foundational models for how internal state and external cues are combined to yield coherent action. Lorenz imagined drives as pressures accumulating in hydraulic reservoirs, released only when key stimuli triggered their release [2] (Figure 1a). Tinbergen instead proposed a hierarchy of control, with higher-order centers suppressing subordinate programmes [1] (Figure 1b).

Modern neuroscience has distilled these theories into circuit motifs for action selection [5,6] (Figure 1c). In race models, evidence accumulates independently in competing pathways, and the first to reach threshold triggers action. Without inhibition, however, multiple behaviors may co-activate. Feed-forward inhibition allows one drive to promote its own output while suppressing others, whereas reciprocal inhibition enforces winner-takes-all outcomes. To reduce wiring demands, the centralized inhibition model proposes a single inhibitory neural node that connects to multiple decision populations. In contrast, a central hub model proposes a decision node that integrates multiple excitatory and inhibitory sensory inputs, with behavioral output determined by their balance and by interactions with parallel decision neurons [5,6].

Uncovering how these motifs operate in male and female brains requires access to discrete circuit components. *Drosophila melanogaster* provides this opportunity. Despite its compact brain ($\sim$140,000 neurons), the fly exhibits rich behavioral repertoires and shares computational principles with mammals [7]. Recent

Figure 1



Models of behavioral control and action selection.

(**a**) Lorenz's hydraulic model conceptualizes motivational drives (sex, hunger, aggression) as a reservoir that builds pressure over time [2]. External releasing stimuli such as the presence of a mate, food, or an opponent act on a valve to channel behavioral output toward feeding, courtship, or escape. (**b**) Tinbergen's hierarchical model organizes behavior into layers: major instincts (e.g. reproduction) at the top level are subdivided into specific modules (e.g. mating, fighting) at a second level and into action patterns (e.g. chasing, singing, copulating) at a third level [1]. Behavioral choice reflects the integration of external cues and internal drives at each level. (**c**) Action selection models. Five circuit configurations illustrate how neural networks could resolve conflicts: a race model where decision neurons (D) are independently driven by sensory inputs (S); feedforward inhibition, where one sensory pathway suppresses competing decision neurons; reciprocal inhibition, where decision neurons mutually inhibit one another; a centralized inhibition selection model where a single central inhibitory neural node (C) interacts with multiple decision neurons; and a central hub model, where a decision center balances inputs from multiple sensory pathways and interacts with parallel decision neurons. (**d**) P1 as a central hub for action selection. Left: balance of inhibitory and excitatory sensory cues on P1 resulting in selection or suppression of courtship. Right: P1 as a central hub balancing courtship with other behavioral drives such as sleep or feeding. S_A, S_B and S_C act as sensory neurons that detect external cues, whereas D_A and D_C function as decision neurons, integrating both external inputs and internal cues. Behavioral output indicates the behavior ultimately selected (A, B or C) for each model. Black arrows indicate excitatory connections, whereas red bars indicate inhibitory interactions. Thicker line weights represent stronger activation or inhibition. Adapted from Ref. [5].

sex-specific reconstructions [8–12], together with genetic tools for recording and manipulating specific neurons [13], now make it possible to dissect behavioral choice at single-cell and synaptic resolution.

In this review, we synthesize advances in understanding how male and female flies resolve conflicts between competing drives. We first highlight sexually dimorphic hubs that integrate sensory cues with internal state to arbitrate between sex, aggression, feeding, and sleep. We then examine sex-survival conflicts, where new work reveals how dopamine dynamically reweights behavioral priorities according to context and goal proximity. Together, these findings illustrate neural principles that link context, internal state, and sex-specific pressures to flexible decision-making.

Sexually dimorphic neural hubs balance sex with competing drives

In *Drosophila*, sexual behaviors are governed by dimorphic neural populations specified by the sex-determination genes *doublesex* (*dsx*) and *fruitless* (*fru*) [14]. Among these, the dsx^+ pC1 cluster has emerged as a central hub for reproductive behavior [15–21]. In males, a subset of ∼20 pC1 fru/dsx^+neurons (P1) integrates social cues, internal state, and prior experience to guide mating decisions [15–17,20,22–26] (Figure 2a). The excitatory-inhibitory balance onto P1 sets the threshold for initiating courtship [15–17] (Figure 1d). Once active, P1 induces a social arousal state that sensitizes males to both courtship and aggression, depending on context [24,27–29]. Transcriptomic profiling shows that P1 neurons express a wide range of receptor types, including those for dopamine, octopamine, and several neuropeptides [30]. This molecular diversity likely enables P1 neurons to flexibly integrate inputs reflecting both internal state and social context.

In females, a smaller dsx^+ pC1 population (∼5 cells per hemisphere [31,32]) acts as an analogous hub, integrating sex-related cues with internal state to regulate receptivity and aggression while sustaining social arousal states [18,19,31,33–38] (Figure 2a). Post-mating, pC1 initiates behavioral responses that increase reproductive success, including courtship rejection and oviposition [18,32,36].

Beyond reproduction, evidence suggests pC1 functions as a shared action selection node in both sexes, arbitrating between mutually exclusive behaviors such as mating, aggression, feeding, sleep and escape [25,27,29,39–43] (Figures 1d and 2b).

Sex vs. fighting

When encountering conspecifics, males must quickly decide whether to court or fight. P1 are central to this choice: weak activation promotes aggression, stronger activation drives courtship [22,27]. This graded control likely reflects functional subdivisions within the broader pC1 cluster [44], with fru^+/dsx^+ P1 neurons promoting courtship and fru^-/dsx^+ neurons outside P1 biasing aggression [29]. Downstream partners further refine these outputs: fru^+ aSP2 neurons integrate P1 and octopaminergic input to promote aggression [45], while other P1 outputs drive courtship [17,23] (Figure 2b). Recent work underscores additional diversity within pC1: subtypes P1a and pC1x are co-activated during male-male-female contests, allowing flies to flexibly alternate between rival-directed aggression and female pursuit [41].

In females, mild pC1 activation enhances receptivity to courting males [19,21], whereas stronger activation drives both receptivity and aggression [19,21,31,35], and even male-like courtship behavior [21]. Like in males, these divergent outcomes likely reflect functional subdivision: pC1a neurons promote receptivity, while pC1d/pC1e drive aggression [18,31,33–36]. Deutsch et al. (2020) proposed that pC1a inhibits pC1d/e, suggesting a lateral-inhibition motif balancing courtship and aggression [31]. Because pC1a is cholinergic, inhibition of pC1d/e may occur indirectly through local inhibitory interneurons or co-transmission by neuropeptides, though this mechanism remains to be resolved.

In both sexes, brief P1/pC1 activation by conspecific cues [15–17] or optogenetics [22,27,31] can trigger a reproductive state that outlasts the stimulus. In males, this persistence relies on recurrent excitatory loops, with pCd and NPF neurons [24,27,28] (Figure 4c). In females, although aIPg neurons do not themselves exhibit sustained activity, their reciprocal connectivity with pC1d/e [31,34,46] or downstream partners may generate persistence through recurrent excitation.

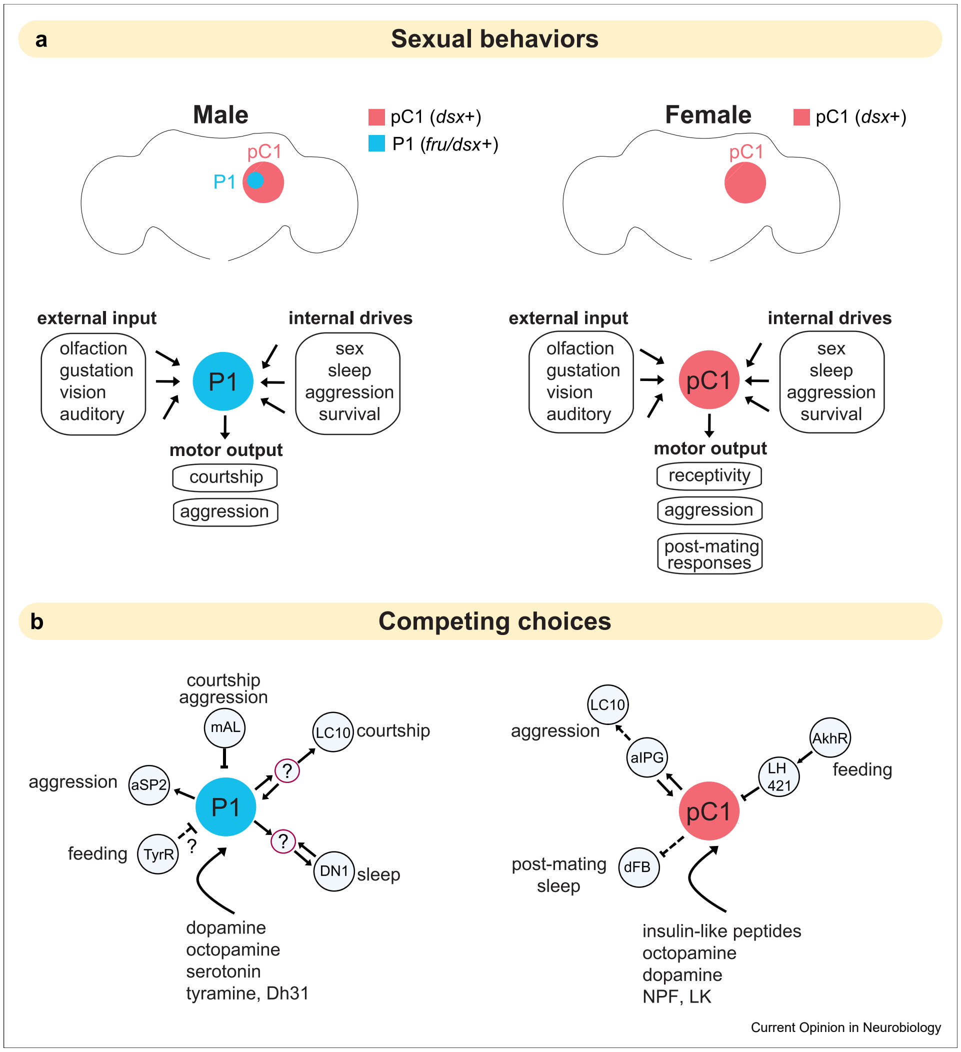
Together, these findings suggest that pC1 hubs arbitrate between courtship and aggression, with graded activity, neural population subtype, and recurrent loops biasing action selection.

Sex vs. feeding

Mating and feeding compete for priority, and nutritional state biases which behavior is expressed. In males, tyramine functions as a satiety signal, exciting courtship-promoting P1 neurons while suppressing $TyrR^+$ feeding neurons [25]. Under hunger and food detection this balance reverses, with $TyrR^+$ neurons activated and P1 silenced, shifting priority toward feeding [25]. This antagonistic co-regulation of opposing pathways provides a general motif for context-dependent arbitration between sex and food.

Endocrine cues reinforce this choice. Sugar intake induces insulin release that inhibits P1; the same pathway

Figure 2



Sexually dimorphic integrator nodes prioritize competing drives.
(**a**) In males, P1 neurons (a *fru*/*dsx*+ subset of pC1) integrate multimodal sensory inputs, internal states, and prior experience to promote courtship and aggression. In females, *dsx*+ pC1 neurons play an analogous role, biasing sexual receptivity, aggression, and post-mating behaviors. (**b**) P1/pC1 integrator hubs arbitrate among competing choices by integrating external sensory inputs and internal states into motor outputs. Examples of neurons that contend with or modulate P1 and pC1 nodes are shown. Neuromodulators including dopamine, serotonin and octopamine, and hormones/peptides flexibly adjust priorities, ensuring behavior is selected according to context. Because the mapping between male and female pC1 subtypes remains incomplete, it is still unclear how exactly these hubs implement common versus sex-specific decisions. Dashed lines indicate suggested connections. Illustrations are based on data cited in the text.

is recruited by non-attractive pheromones, where ppk23 gustatory neurons trigger insulin via the CCAP peptide to suppress inappropriate courtship [47]. Gut enteroendocrine cells release Dh31 after feeding, acting on distinct Dh31R^{+} brain neurons: one suppresses feeding, the other promotes courtship [48]. Thus, gut-brain and pheromone signals converge on endocrine pathways to align nutrient state with reproductive opportunity.

In females, starvation reduces sexual receptivity to courting males [42,49,50]. Here, hunger signals recruit AkhR^{+} octopaminergic neurons, which activate LH421 interneurons to inhibit pC1 via GABA signaling, suppressing receptivity [42] (Figure 2b). Feeding rapidly restores sexual behavior. Because pC1 also integrates male song, pheromones, and reproductive status [18,19,31,32,36,37], it acts as a hub where metabolic and reproductive cues converge to regulate female choice.

Post-mating, feeding priorities diverge: females increase yeast intake to support egg production [51–53], whereas males transiently suppress yeast consumption to prioritize fitness [53]. Anterior leucokinin (ALK) neurons mediate this switch in a sex-specific manner. In females, mating triggers ALK neurons to release leucokinin, driving yeast appetite [53]. In males, ejaculation-induced corazonin activates ALK neurons to release sNPF, which suppresses yeast feeding via FB-LAL neurons [53]. Female FB-LAL neurons are dispensable, highlighting distinct peptide pathways underlying sex-specific strategies.

Sex vs. sleep

Animals face a fundamental conflict between sleep and reproduction: sleep restores fitness, but courtship demands wakefulness. In males, the presence of females suppresses sleep in a state-dependent manner: sexually aroused males stay awake, whereas sexually satiated or sleep-deprived males favor sleep [39,40,54,55]. This switch is mediated by reciprocal interactions between P1 and sleep/arousal circuits [39,40,54,55]. P1 biases behavior toward courtship via circadian DN1 neurons [39], which inhibit sleep through Dh31 signalling [56]. P1 and DN1 are thought to form mutually excitatory loops that sustain wakefulness [39] (Figure 2b).

Upstream, male-specific octopaminergic MS1 neurons both suppress sleep and activate $FruM^{+}$ circuits, reinforcing courtship [54]. Nutritional state gates this balance: protein-deprived males no longer suppress sleep in response to female cues [55]. This shift is mediated by dopaminergic neurons projecting to the protocerebral bridge (DA-PB), which act downstream of P1 to promote wakefulness, but only when protein is sufficient, ensuring mating effort is invested under favorable conditions [55].

Whereas males suppress sleep when mating opportunities arise [40,54,55], females do so only after copulation [57]. Male sex peptide transferred on copulation reduces siesta sleep via SPSNs and SAG neurons [57], reallocating time to feeding and egg-laying. Post-mating sleep plasticity also depends on female pC1 neurons inhibiting sleep-promoting dorsal fan shaped body (dFB) neurons [43]. This effect depends on diet: sleep is suppressed on protein-rich food but not on sucrose alone [43], so rest is sacrificed only when conditions support egg laying.

Natural variation in sleep further underscores sex differences: short-sleeping male flies court more, whereas female oviposition is largely unaffected [58], indicating that reproductive output in females is less sensitive to sleep and circadian disruption [59].

Dopamine updates priorities based on context and goal proximity

Dopamine has long been studied in associative learning and memory [60], yet its functions extend far beyond reward prediction. Across species, dopaminergic neurons integrate external cues, internal states, and ongoing behavior to update decisions as contexts shift [60–62]. In *Drosophila*, this flexibility is most evident in reproduction-survival trade-offs [61,63], where it dynamically reweights priorities as mating unfolds.

Sex vs. escape

Dopamine filters sensory inputs to sustain courtship as mating approaches

Survival and reproduction often conflict: caution helps ensure survival, but risks lost mating opportunities, while persistence enhances reproduction at the cost of safety. Male flies switch between escape and reproductive priorities based on mating proximity [61]. During early courtship, predator-like threats activate LC16 visual projection neurons [64], which recruit serotonergic $5\text{-HT}^{\text{PMPD}}$ neurons to suppress P1 and pIP10 courtship nodes, biasing behavior toward escape [61] (Figure 3a). As males progress through courtship, dopaminergic activity ramps in PPM1/2 neurons, inhibiting LC16 via Dop2R and overriding serotonergic suppression of P1 [61] (Figure 3b and 4a). This produces a transient “love-blind” state in which danger cues are ignored when mating is imminent.

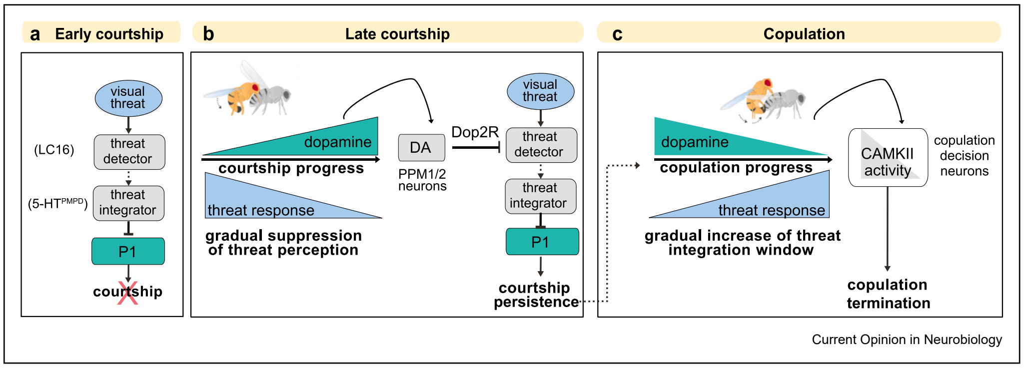
Although classically linked to reward prediction in mammals [60], work in flies reveals a distinct role for dopamine ramping: functioning as a sensory filter that suppresses competing cues and enables animals to prioritize imminent goals during conflict [61]. Similar principles may operate in rodents, where dopamine in the striatum facilitates avoidance in threat-reward conflicts [62].

Dopaminergic ramping in male flies is driven by late courtship movements, such as abdomen bending [61], though female sensory cues are also likely to contribute. How this ramping arises; through spontaneous activity, intrinsic excitability, or synaptic integration remains unresolved. It is also unclear whether PPM1/2 neurons selectively gate visual threats or broadly suppress other sensory modalities, and whether such dopaminergic filtering extends beyond the mating context.

Additional modulatory mechanisms likely act in parallel to bias behavior towards courtship. Sexual arousal due to increased P1 activity gates the perception of female visual cues [65], possibly via TuTuA neurons [46], enhancing pursuit (Figure 4b). Once engaged, recurrent excitation sustained by dopaminergic aSP4/PAL neurons likely maintains courtship motivation [24,26,28].

Unlike PPM1/2, P1 activity does not ramp [15], raising the question of whether recurrent loops and ramping represent parallel mechanisms or converge downstream.

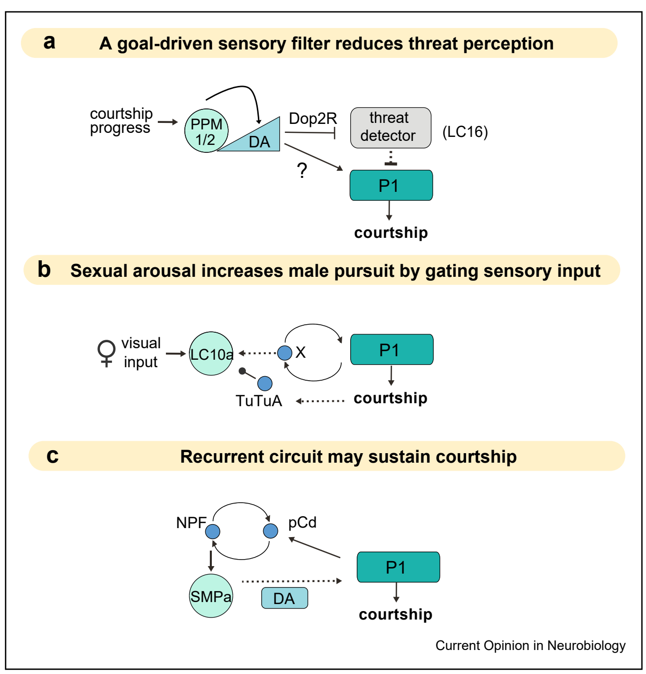
Figure 3



Dopamine recalibrates behavioral priorities across mating states.

(**a–b**) A dopamine-governed filter mechanism reduces threat perception as mating approaches. (**a**) Early in courtship, visual threats detected by LC16 neurons activate serotonergic PMPD neurons, which inhibit central courtship nodes P1 (via 5-HT7) and pIP10 (via 5-HT2B), biasing behavior towards escape [61]. (**b**) As courtship progresses and copulation attempts begin, PPM1/2 neurons ramp their activity. Dopamine (DA) ramping suppresses the LC16 visual threat pathway (via Dop2R), suppressing threat perception and allowing males to prioritize courtship when copulation is imminent [61]. (**c**) Dopamine modulates copulation persistence through ventral nerve cord circuits [63]. At the start of mating, strong dopamine input facilitates CaMKII activation in copulation decision neurons (CDNs), narrowing their window for integrating termination signals and thereby maintaining persistence even during threats. Later, as dopamine tone declines, CaMKII activation is reduced, broadening the integration window so repeated threats accumulate, increasing the likelihood of termination once fertilization is secured. Dashed lines indicate indirect connections.

Figure 4



Proposed mechanisms to sustain courtship persistence despite threats

(**a-c**) Circuit summary of three proposed mechanisms sustaining courtship persistence despite threats: (**a**) Goal-driven sensory filter: PPM1/2-derived dopamine (DA) attenuates LC16 inhibition of P1, reducing threat perception as mating approaches [61]. (**b**) Arousal-gated vision: P1 boosts LC10a visual inputs [65], likely via TuTuA neurons [46], to enhance female pursuit (**c**) Persistence loop: recurrent interactions between P1 and SMPa/partner nodes, reinforced by dopamine, maintains courtship motivation [24,26,28]. Dashed lines indicate suggested or indirect connections.

Unlike males, females do not perform a progressive courtship sequence but signal receptivity by slowing and opening the vaginal plates [18]. Dopamine contributes to receptivity [66], yet its role in sex-survival arbitration is unknown. Because females must survive to lay eggs, they may be under stronger pressure to escape than males, and PPM1/2 ramping could therefore be absent, biasing them toward survival. Consistent with this, parasitoid exposure suppresses oviposition [67], and mating engages dopamine-mushroom body circuits that enhance attraction to nutrient-rich odors, biasing post-mating foraging and oviposition to support offspring development [68].

Dopamine sets integration timescales to allow escape in late copulation

Threat responses also shift as copulation progresses [63]. Although sperm transfer is completed after ∼6 min, males benefit from prolonging copulation (up to ∼20 min) to block mating rivals. During the first several minutes, flies almost completely ignore threats such as heat pulses and wind gusts, even at the risk of death, presumably to ensure fertilization. Sensitivity returns gradually and after ∼15 min flies respond more strongly to threats. As certainty of mating success increases, males become more likely to terminate copulation.

This shift is mediated by dopamine acting on copulation decision neurons (CDNs) in the abdominal ganglion. Early in mating, dopamine boosts CaMKII excitability in CDNs, shortening integration time windows so that only strong, sustained threats trigger termination. As dopamine wanes, the window expands, increasing termination likelihood (Figure 3c). These findings reveal that motivation can bias decision-making not only by scaling sensory inputs, but by tuning the temporal integration of information within decision circuits.

Open questions remain about how dopamine couples to CaMKII, which pathways convey threat-related input to the CDNs, and whether integration-window tuning is a general strategy across other decision bottlenecks. In females, acceptance-rejection is under dopaminergic and GABAergic control [66] but how threat exposure dynamically updates these circuits remains unexplored.

Dopamine's role in other reproductive trade-offs

Beyond escape conflicts, dopamine biases other reproductive trade-offs. Under nutrient deprivation, dopaminergic signals downstream of P1 prevent courtship-related sensory cues from overriding sleep until feeding is restored [55]. Oviposition is likewise under opponent dopaminergic control. PAM/PPM3 neurons bias females toward ethanol-rich sites, while PPL1 neurons drive avoidance, balancing ethanol's potential benefits against toxicity [69]. Females search for suitable egg-laying sites over minutes, while oviDN neurons gradually ramp their activity until reaching a threshold that triggers egg deposition [70]. Ramping is faster on high-value substrates and slower on poor ones, implementing a rise-to-threshold process for value-based choice [70].

Concluding remarks

Understanding sexually dimorphic decision-making demands insight into how neural circuits govern behavior, how they interact, and where they diverge between the sexes. *Drosophila* offers a uniquely powerful platform: sex-specific connectomes [8–12] and refined genetic tools [13] allow networks to be mapped at synaptic resolution and dimorphic nodes to be identified with precision. These resources are beginning to reveal how competing drives are weighed, how persistent states arise, and how internal state and context flexibly tune action.

Action selection circuit principles are emerging. In sex-feeding conflicts, feed-forward inhibition has been identified as a key mechanism, whereas in sex-sleep conflicts reciprocal inhibition plays a prominent role. Central hubs such as pC1/P1 integrate multimodal sensory inputs with internal states to bias motor programmes toward reproduction, aggression, feeding, or escape [25,27,29,39–43,54,55,61]. Subsets of these neurons specialize, for example, responding selectively to one sex, but interact to coordinate related behaviors. Yet pC1 is a highly heterogeneous population [44], and incomplete cross-sex mapping leaves the correspondence between male and female neural subtypes, and their role in sex-specific arbitration, unresolved.

Behavioral priorities are dynamically tuned by neuromodulation. Acting through specific receptors, neuromodulators reconfigure circuits to promote one action while suppressing others. Dopamine exemplifies this flexibility during sex-survival conflicts. In male flies, ramping dopamine filters out competing inputs to sustain reproductive pursuit, while its decline later in mating reopens the window for threat-driven escape [61,63].

Progress is limited however by a persistent bias: most studies examine one sex in isolation. Direct male-female comparisons in matched behavioral contexts are urgently needed to reveal where circuits and mechanisms are conserved or have diverged. Molecular profiling and single-cell atlases [30,71–73] promise to uncover new dimorphic nodes and neuromodulatory pathways, linking gene expression to circuit function. Other layers of modulation, such as gut-brain signalling [74], organ geometry [75] and reproductive physiology [76] remain underexplored yet influence behavioral choice.

Conflicts between drives like mating, feeding, and danger avoidance are fundamental challenges across species. Like pC1/P1 neurons in flies, central hubs such as VMHvl neurons in mice integrate sex-related cues and social context, generate scalable persistent states, and regulate both reproductive and aggressive behaviors [77]. In both flies and rodents, dopaminergic activity ramps with goal proximity [60,78] and functions in conflict resolution [61,62]. Such parallels suggest that fly studies are not about charting idiosyncratic micro-circuits in a compact brain but about revealing general algorithms for behavioral choice: how to persist when a goal is near, how to switch when conditions shift, and how sex-specific priorities recalibrate the balance.

Declaration of competing interest

The authors declare no competing financial or personal interests that could have influenced the work reported in this article.

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Data availability

No data was used for the research described in the article.

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** of outstanding interest

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The first whole-brain connectome of an adult female *Drosophila* (139,255 neurons, 54.5 million synapses) provides an unprecedented resource for tracing pathways from sensory inputs to motor outputs. Comparison with the forthcoming male connectome will enable direct analysis of sex-specific circuit architectures and their behavioral consequences.

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