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What is a decision?

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In a discussion about what decisions are, John Krakauer emphatically pronounced that "decisions happen for reasons", in answering 'no' to my question if it wasn't a decision with which foot to start walking from a stand-still.

A recent article from the laboratory of Carolina Rezaval in Birmingham studied a decision-making process in male *Drosophila* fruit flies where the reasons for each decision seemed apparent. When a male fly was presented with a looming stimulus (which mimics a threat from a nearing predator) while in the early stages of courtship, it stops courting and either freezes or tries to escape. In later stages of courtship, however, the same threat stimulus is no longer able to interrupt courtship and elicit escape. While it is less clear if the male fruit fly is able to articulate them, the reasons for him to behave in that way seem obvious: in the early stages of courtship, the male escapes as it is still not clear if the courtship attempts will be successful. In a later stage, once sufficient information has accumulated about the receptivity of the female and/or copulation is close, it's worth trading some safety for the prospects of getting one's genes into the next generation. In biology, such reasons are commonly called "ultimate causations" of the behavior, while the neurobiology by which they are implemented are the "proximate causations". The recent article concerned the proximate causations of these decisions in *Drosophila*.

In the early stages of courtship, the authors found, a class of visual neurons in the fly's optic lobe called LC16 detect and respond to the threat stimulus. Via several other neurons, these LC16 neurons connect to P1 neurons in the fly brain, which collect multimodal information (e.g., female sensory cues) and can mediate courtship behavior. If LC16 neurons are activated by a threat stimulus, downstream neurons release serotonin, which inhibits the P1 neurons, halting courtship. This inhibition between different behavior circuits is a common theme observed in many other preparations, preventing two behaviors occurring at the same time. In this case, LC16 neurons mediate escape behavior and inhibit other behaviors, such as courtship, which could interfere with the escape.

The fact that LC16 no longer inhibits courtship at later stages implies that there is more to this story than the simple inhibition known from so many other experiments with different animals. In the course of courtship, as the duo gets closer to copulation, a population of dopamine neurons in the male slowly ramp up their activity. These dopamine neurons make direct synaptic connections with LC16 neurons and inhibit them. In other words, the lack of escape is not due to a failure of LC16 to inhibit courtship, but due to a failure of LC16 to respond to threat stimuli.

Taken together, much like what was known from other preparations, there is a mutual inhibition between circuits mediating different behaviors: escape behavior circuits inhibit courtship circuits and courtship circuits inhibit escape circuits. Until now, such mutual inhibition was mainly studied in central-pattern-generator driven behaviors such as swimming/feeding in molluscs (cited by the authors). In these cases, the inhibition was identified very close to the motor side of the circuits. In the case of male *Drosophila*, the relation of the neuronal processes appears much closer to sensory input: Both LC16 and P1, while not being sensory neurons, respond to sensory stimuli: LC16 to visual threat and P1 to female sensory cues. Their inhibition can be interpreted as a lack of sensation. The authors themselves do not seem to have made up their minds about this. While they start their article by emphasizing the animals' "decisions that require balancing opportunities and risks", title and abstract of their work invoke more attention-like processes by using words such as "love-blind". Which is it, decision or attention?

Is the decision to court or to escape really a decision, where the "risks and opportunities" are weighed and then one of the two options is chosen, or is this just an example of sensory competition, where eventually one "blinds" the other, such that the losing stimulus is simply not perceived? If only one of the two options is perceived, it can no longer be a decision, can it? As neither LC16 nor P1 are directly involved in sensing the stimuli, it is fair to assume that both the looming stimulus and the female sensory cues are processed appropriately even if any of the two classes of neurons are inhibited. However, if the perceived looming stimulus is not longer assessed as a threat, or the female sensory cues no longer perceived as sexually attractive, aren't the animals then just simply responding to the single remaining stimulus, without needing any reasons? As an aside: if so, what are the 'losing' stimuli perceived as?

The flies cannot tell us what they perceive and how, but this is not the first time an animal's behavior that outwardly looks, sounds and smells like a decision, loses these properties upon neuronal inspection. Leeches commonly respond with local bending of their body wall to mechanosensory stimulation such as light touches. Increase the intensity of the touch a little, and the animal will start crawling away from it, and with further increases, the animal will start swimming to escape. However, when the animal is feeding, not even the strongest mechanosensory stimuli can get the animal to do swim or crawl away. The reasons for this decision are clear: if the leech has itself attached to the animal it is sucking blood from then this animal is likely moving around in the pond or stream where the leech lives. Given the common environments for this leech species with plenty of vegetation in the water, the moving animal will likely touch an number of obstacles and chances are that these obstacles will also touch the leech. If it were to start crawling away or even swim away in that phase, it would not be able to obtain a sufficient blood meal for survival and procreation. So the leech will literally hold on for dear life until it has had a sufficient meal.

Decades of research have provided a pretty good understanding of the circuitry for the processing of mechanosensory stimuli in the leech. Way back in 2009, Gaudry and Kristan reported on the neuronal mechanisms underlying the decision of feeding leeches to ignore mechanosensory stimuli. Analogously to the male flies where a sufficiently progressed courtship inhibits the transmission of threat stimuli, feeding in the leech also leads to the release of a biogenic amine, in this case serotonin. Serotonin then inhibits transmitter release from the mechanosensory neurons. Conceptually very similar to the male flies, the sensory stimuli are still perceived by the relevant sensory neurons, but the transmission of the signal is blocked via central processes. In male flies, dopaminergic neurons active during courtship inhibit threat transmission during courtship, in the leech, serotonergic neurons active during feeding inhibit mechanosensory transmission during feeding. In the case of the leech, the authors take an unambiguous position: Title, abstract and text all call the inhibition of responses to mechanosensory stimulation during feeding a ‘choice’ or ‘decision’.

In both flies and leeches, their behaviors were tied closely to sensory stimuli: looming stimuli, female cues, blood, touch. It is precisely because of these stimulus situations, that we can articulate the reasons for the decisions the animals make. The animals’ decision appear very “reasonable” for the human observer. However, the two examples above are just two of a growing list of examples where this very intuitive sense of the behavior being a “decision” starts to disappear with our understanding of how the neurons are doing it. If one of the two stimuli the animal has to decide about gets shut out so that only one remains, where is the decision?

A classic example of a decision in humans is “red or white wine?” If human nervous systems would mediate such a decision analogously to flies and leeches, the decision would be that between, say, an empty glass and a glass filled with wine – very different from how we envisage and experience such decisions. But then again, the decisions studied in the examples above are life-and death decisions for the animals. Everybody knows that decisions about loved-ones are clouded by our love – the world “love-blindness” exists for a reason. Everybody has experienced products in a grocery store becoming much more attractive when we are hungry. It is conceivable that our minds similarly bend our sensory experiences when in a life-threatening situation. If the animal examples were anything to go by, decisions with reasons would more like reactions to stimuli and less like actual decisions?

One can think of two arguments why studying the neurobiology of decisions without reasons may actually be a more fruitful endeavor for understanding decision-making, one conceptual and one practical.

Conceptually, as long as we haven’t understood the whole process, we can never be sure how much choice any human or animal ever has in a given situation. We simply cannot know how coercive, ahem, compelling the reasons for the decision actually are. Practically, it is also not the most efficient way to just study one decision after another until one happens to stumble upon one where the ‘reasons’ aren’t really just competing stimuli eliciting responses where, ultimately, one wins in a very deterministic way. And even if one finds such a lucky situation, as is seems to be the case with photopreference in flies, even then the practical problem remains, that without complete knowledge of sensory processing, it is exceedingly difficult to know if one’s manipulations are actually affecting the decision-making process itself or just some aspect of sensory processing.

A decision involves that there actually are at least two real options. In the animal examples above, it looks, to the observer of the behavior, like there were two such options, but once the neuronal mechanisms mediating the ‘choice’ have become clear, one of the options was gone. This is not the case when studying decisions that have no reasons at all. Under such circumstances, the decision is always 50-50. The outcome is, if the experiment is properly designed, unpredictable and happens exclusively in the animal and cannot be dictated by external stimuli. There are many such examples: isolated buccal ganglia of the sea slug *Aplysia* produce different motor programs in a petri dish, without any sensory organs. Analogously, isolated leech nervous systems start and stop producing swimming motor programs in the dish. Tethered fruit flies produce different flight maneuvers even if flying stationarily inside the center of a ping-pong ball. In these cases, there are no obvious, outwardly discernible 'reasons' for the animals/nervous systems to pick one behavior over another. The reasons for the decision come solely from within the animal itself. Conceptually, these situations appear much closer to what we call "decisions" and practically, they avoid the sensory confounds altogether.

These two kinds of decisions have traditionally been referred to as "picking" and "choosing" in a 1977 seminal paper by Ullmann-Margalit and Morgenbesser.

So what really is a decision and how do we study them in neuroscience? Picking or Choosing?

In human psychology, there is a distinction between "judgments" and "decisions" (i.e., the judgment and decision-making, JDM, framework):

> *'Judgments' refer to how individuals acquire and process information to arrive at an understanding of the situation or state of the world. 'Decisions' refer to the processes by which individuals use judgments to arrive at a course of action. In other words, individuals can vary in two main ways: how they 'see' the world, and what they decide to do about it.*

It appears that the leech and fly work cited above merely concerns the "judgment" aspect of JDM, leaving the decision-making untouched. In this JDM framework, does it not seem wise for neuroscience experiments to circumvent the practical problems of judgments by studying decisions that happen in the absence or at least with equivalence of sensory stimuli?