UNDERSTANDING HUMAN COGNITION: THE COGNITIVE NEUROSCIENCE OF MOTOR LEARNING

Interview with Professor Richard Ivry

Professor Richard Ivry[1]

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Dr. Richard Ivry *is a Professor of Psychology and Neuroscience in the Department of Psychology and the Helen Wills Neuroscience Institute at the University of California, Berkeley. He directs the Cognition and Action (CognAc) Lab. The CognAc Lab employs a diverse array of approaches, from classic psychological experiments to computational modeling and fMRI, to explore the cognitive neuroscience that underlies skilled movement. In this interview, we discuss his findings on the influence of task outcome in implicit motor learning and the neural signatures of prediction errors.*

BSJ: What is cognitive neuroscience?

RI: Well, I'm trained as a cognitive psychologist. Cognitive psychology is building models of the mind: how do we think, how do we use language, and how do we perceive objects? These questions are usually addressed in terms of psychological processes. Cognitive neuroscience was a real new push in the early 1980s which recognized that we can use neuroscience methods not just to describe what part of the brain does something, but actually use that neuroscientific information to help shape our psychological theories.

So, whereas behavioral neurology is solely interested in what part of the brain does what, cognitive neuroscience is the idea that not only can we use insights from our psychological experiments to understand how the brain works, but we can also then take the insights from studying the brain to build psychological theories. That's the essence of cognitive neuroscience—it is a bidirectional interest.

BSJ: What initially drew you to the field?

RI: I was in the right place at the right time. I entered graduate school in 1982 at the University of Oregon. One of the pioneers in the cognitive neuroscience movement, Mike Posner, was there (and is still there) as a professor. He was just starting to do research with people who had brain lesions, and he worked with stroke patients who had disorders of attention. He was interested in showing how you could use sophisticated cognitive experiments to build models of attention.

I was in the right place to not only learn from him, but to realize that we could apply a similar strategy in studying movement disorders to understand how people perform skilled movements. I just landed happily in a graduate program as things were taking off.

BSJ: We read your paper on the influence of task outcome on implicit motor learning. Could you define implicit versus explicit learning for our readers?

RI: Tracing it all the way back to Freud, one of the most fundamental distinctions in psychology research is the notion that much of our mental life is occurring subconsciously, as opposed to consciously. Freud tended to frame this distinction in terms of a battle between the conscious and the unconscious. The unconscious was all your desires, and the conscious was the way to keep a check on things.

But I don't think it's two armies battling each other, although I think it's quite obvious that we're only aware of a limited amount of our mental activity. Right now, I'm sure that everything in this room is activating sensory systems. Probably percolating somewhere in my brain is the thought of getting ready for my first Zoom class at one o'clock this afternoon. I'm only aware of a limited amount of that information. So that's the fundamental question: why is there a limit on what we're aware of?

Setting that aside, our interest in human performance, at least in terms of motor control, is recognizing that when we learn a new skill, much of the learning is implicit. For instance, we can certainly benefit from coaching. In baseball, the coach tells you how to orient your shoulder to the pitcher, how to hold the bat, and so on. This information is the essence of something being explicit—I'm aware of it. If I'm aware of it, I can tell someone else about it. But a lot of that skill learning is really implicit, as in, "I can't quite put my finger on it." The classic example here is bicycle riding. It's really hard to tell a person how to ride a bicycle. You can try to coach someone, but in the end, it basically comes down to giving them a shove and letting them go across the playground. The body figures it out.

Lots of our memory is implicit. I'm not aware of all the different memories that are being activated; they're all just churning around and away in my brain. As you say a word, all the things I associate with it get activated, but I will only become aware of some of that information. So whatever domain you study, whether it's tension, memory, or motor control, there are always things happening at both the explicit and the implicit level. What we observe when someone performs a skilled behavior is the sum of those processes. Our research has been aimed at trying to dissect these skilled behaviors to determine the characteristics of what you can learn implicitly versus explicitly, as well as the brain systems that are essential for one type versus the other and how they interact.

BSJ: Some previous studies concluded that reward has no effect on the rate of learning, while others concluded that reward does have an effect. What do you think led to these inconsistencies?

RI: In the classic case, experiments that study these effects perturb the world in some way. In the laboratory we would certainly like to study real, natural skill development, but that's a pretty difficult process. So, we usually try to make more contrived situations where we can accelerate that learning process, to do it within the confines of a one-hour experiment. In any learning situation, it's quite likely that you could have both explicit and implicit processes operating, and it may be that reward only affects one of those two. So one account of the inconsistency is that in the older literature, they didn't really have methods to separate the different contributions of the different learning systems.

BSJ: What is clamped visual feedback, and how did you use it to isolate implicit from explicit learning?

RI: If I reach for your phone, I'm getting feedback. I see how close my hand is to the phone. We can easily replace the hand with some proxy. This is what you do every time you're on your computer and move your mouse. You move your mouse to click someplace. You're using feedback because you recognize that your movements of the mouse are corresponding to the movement of the cursor.

It's very easy for the human mind to accept that a moving cursor is representative of their hand position. If we want to create a perturbed world to study learning, we change this so that whenever you move your hand, the cursor becomes offset by 45 degrees. Then we can ask, "How do people adjust their behavior to compensate for that?" It's what you're doing all the time with your mouse anyhow. In this "game," sometimes a small movement with the cursor takes a big movement of the mouse, or a big movement of the mouse is a big movement of the cursor. You very quickly adapt.

Clamped feedback is fixed feedback. It's the idea that we can fool the implicit system to think that the cursor is where the

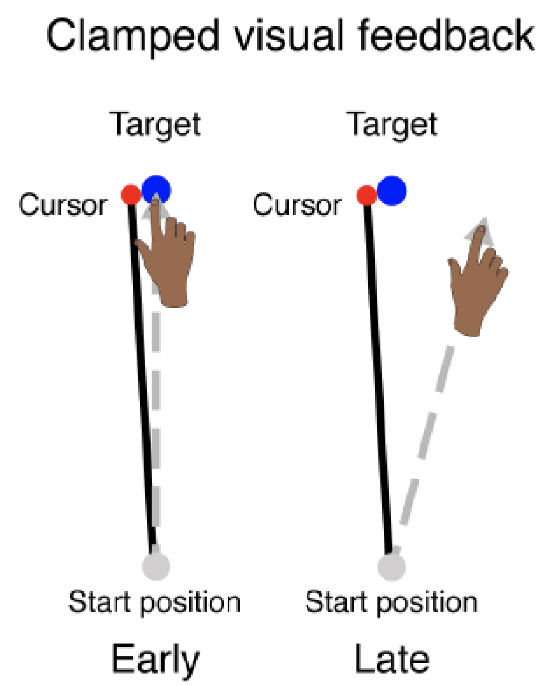

Figure 1: During clamped feedback, the angle of deviation between the cursor and target remains constant. *The difference in hand angle to the target depicts adaptation to the clamped feedback over the course of the experimental period (early to late). If the cursor is consistently to the left of the target, adaptation will result in hand angle increasing to the right (Kim et al., 2019).*[2]

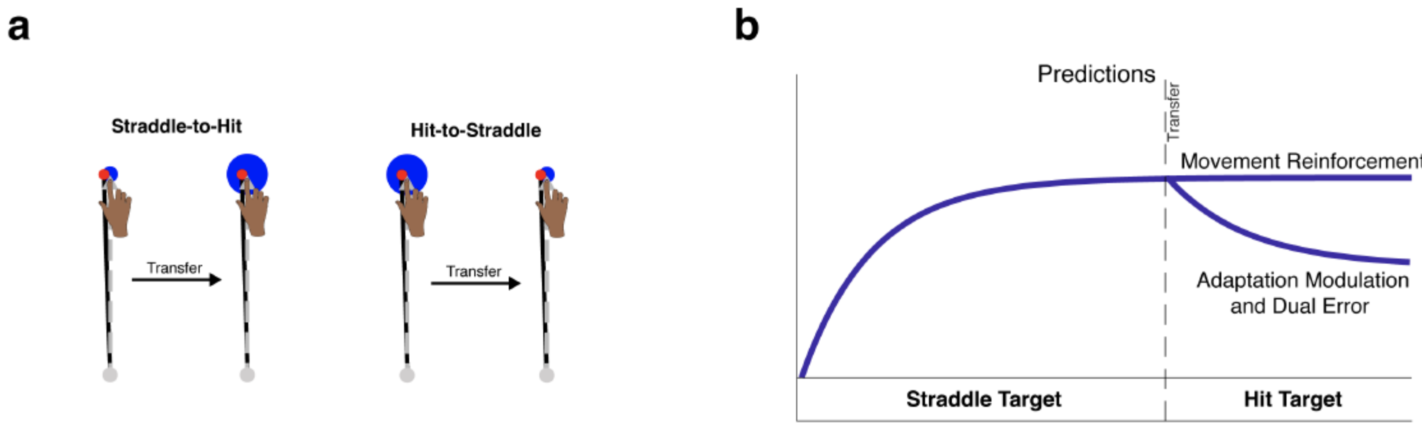

Figure 2: To distinguish between the three models, after an initial period of adaptation, subjects were "transferred" to a different target size. *The size of the target is either increased (straddle-to-hit condition) or decreased (hit-to-straddle condition). As depicted in part (b), where the y-axis represents hand angle, the movement reinforcement makes different predictions for this experiment than the adaptation modulation and dual error models (Kim et al., 2019).*[2]

hand is, even when you are explicitly aware that it isn't; no matter where you reach, the cursor's always going to do the exact same thing. This very primitive implicit motor learning system might not have access to that information, and it will respond as though it is the feedback. If I reach somewhere but the cursor tells me that I'm somewhere else, then I'm going to gradually correct my movement. The clamped feedback seems to be picked up by the motor system to recalibrate, even though I have no control over it (Fig. 1).

We set up our experiment so that motor error would vary. The motor error is the discrepancy between the dead center of the target and where the cursor goes. We assume the motor system demands perfection. It really wants you to be right on the center of the target, so the motor system is going to respond to this error. The reward manipulation happens by using a big target or a small target. If it's a small target, the clamp lands outside. That looks like an error. Not only did the cursor not go where you expected it to, but it missed the target. For the big target, it still didn't go where you expected it to, because you're probably aiming for the center. It goes off to the side, but it's still within the target. So you have this contrast between "Did you hit the target? Or did you miss the target?" Then you can ask how that changes how much learning is observed, how much adaptation occurs as the result.

What was surprising to us was that the amount of adaptation was really reduced in trials with a big target. For a variety of reasons, it was previously thought that the implicit system didn't care about reward. And yet, the output of that implicit learning was attenuated when you hit the target. So we thought that reward might be attenuating how much you learn.

BSJ: Can those results be generalized to different conditions? For instance, would you expect to see similar results if variables like hand angle were altered?

RI: I think the results can be generalized. Since our paper came out, other groups have picked up on this question and have been testing different manipulations. The favorite one these days is that I reach towards a target, but as I'm reaching, the target jumps to where the clamp is, which the person knows they have no control over. You see a similar attenuation under those conditions.

It's like how the study of illusions has always been very useful to help us understand how perceptual systems work. Even when we know about them, we still see the illusions, and that is because they tell us something fundamental about how the perceptual system is organized. We'd like to think that the same thing is true here—we're able to isolate a system that's constantly happening. Every time you put on your jacket, it's a little heavier when you have to reach for something than when you don't have that jacket on. The motor system has to constantly be recalibrating, right? So our belief is that this system is always operating at this implicit level, commanding perfection and making subtle changes to keep yourself perfectly calibrated.

BSJ: How do the movement reinforcement, adaptation modulation, and dual error models differ in their explanations of how reward and error affect learning?

RI: So we came up with hypotheses about different learning processes, each one subject to its own constraints. We have to specify what we really think is happening, and then by writing the computational models we can make quantitative predictions based on results. Sometimes, unexpected things come out of modeling.

The first model, the movement reinforcement model, just says that there's one learning system driven by errors and another driven by rewards. It basically is the classic sort of reinforcement learning model in the brain where if I do something, I get rewarded to do it again. So the first model says there are two different systems operating, one regarding independent learning and one that just reinforces rewards, and that actions and behaviors are the composite of those two. But that model makes predictions that don't hold up very well.

The second model, the adaptation modulation model, shows a direct interaction between learning systems—I have an error-based system, and I can turn the strength up and down depending on reward. The third model, the dual error model, says there are two separate implicit learning systems that independently operate, where one system cares about whether my hand went where I wanted it to go (that's the sensory prediction error), and another system cares about whether I achieved my goal. Performance is the sum of their two outputs.

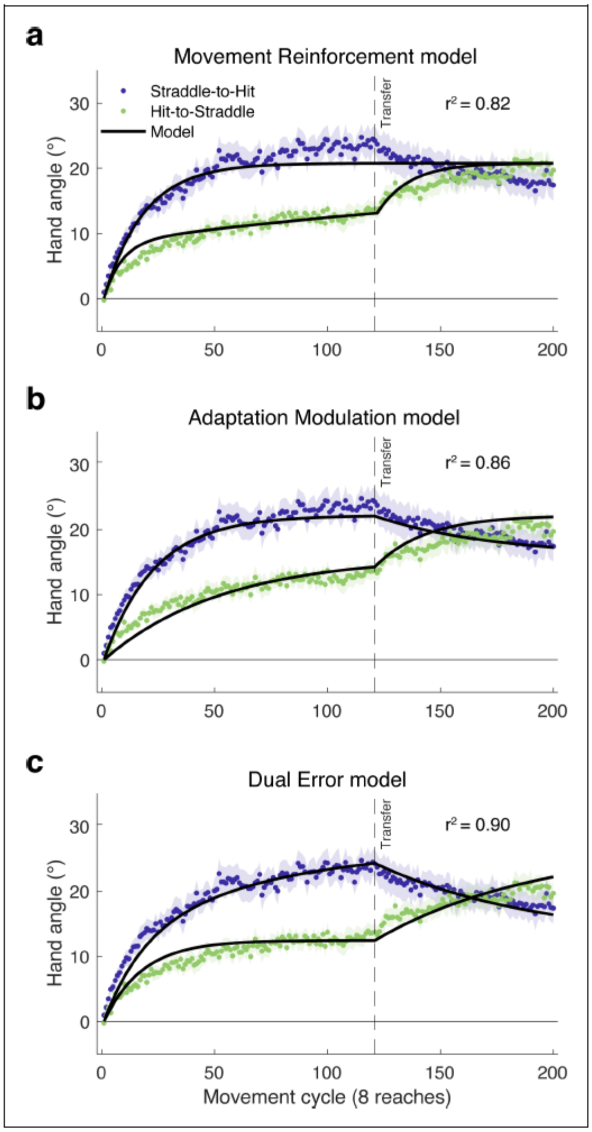

Figure 3: Black lines are predictions made by the movement reinforcement model (top), adaptation modulation model (middle), and dual error modulation model (bottom). *Purple and green dots are experimental data, representing the straddle-to-hit and hit-to-straddle conditions, respectively. As demonstrated by the discrepancy between the black line and the dots in part (a), experimental data fails to align with predictions made by the movement reinforcement model (Kim et al., 2019).*[2]

BSJ: What did your experiments suggest about the accuracy of each of these three models? How were you able to differentiate between them?

RI: Well, we weren't able to differentiate between the last two models. We saw that once you start hitting the target, the amount of adaptation decreases. That's how we can rule out the first model, due to a qualitative difference between the prediction and the result (Fig. 2, Fig, 3).

It's more of a quantitative distinction between the dual error and the adaptation modulation model. We just didn't have good enough data yet to distinguish between the two, so that's why we continue on the project, having to come up with new experiments to differentiate between those models, or find out that they're both wrong and find some other alternative.

BSJ: We also read your paper on neural signatures of reward prediction error.[3] Could you explain for our readers what reward prediction error is, and its relevance in understanding human cognition?

RI: Sensory prediction error is what we typically think of as motor system error. I expect that when I reach for this phone, I'm going to grab it. If I miss, I call it a sensory prediction error. I have an expectation of what I'm going to experience, and what I'm going to feel. If what I feel is different than what I expected, that's a sensory prediction error. It is used to recalibrate the motor system to improve your movements in a very fine-tuned way.

A reward prediction error is when I have an expectation of how rewarding something's going to be. For example, I go to Peet's Coffee and order a latte, and I have an expectation of what a latte tastes like. But there's a lot of variability in those baristas. Say I get one of the bad ones. I take a sip of the coffee, and it's a badly-made latte. That's a negative prediction error. I had my expectation of what it tastes like, and it wasn't as good, so I didn't get the full reward I cared about. If it happens consistently, I'm going to use those prediction errors. Sometimes I get a great coffee, so I'm going to figure out which coffee shops I like and use those reward prediction errors to help me make choices in life. The reward prediction error influences our choices, while the sensory prediction errors are more of, once I made a choice, whether I actually succeeded in accomplishing the desired action. It's a distinction between selection (the reward prediction error) and execution (the sensory prediction error).

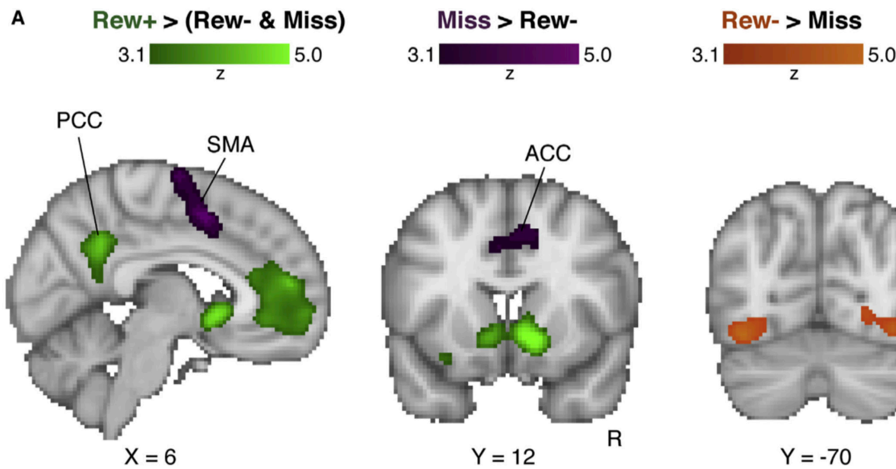

Figure 4: Regions of the brain implicated in reward prediction error, determined by fMRI. *Note that many of these regions are localized to the frontal lobe (McDougle et al., 2019).[3]*

BSJ: What parts of the brain are thought to be involved in reward prediction error, and how do their roles differ?

RI: To have a reward prediction error, I have to have a reward prediction. So what's my expected outcome? Staying with the Peet's Coffee example, I have an expected reward for getting a latte at one Peet's, and I have a different one for getting it at another Peet's. That represents what we call the value; I think one Peet's location is more valuable than another. Then we need a system that actually processes the feedback, to recognize if I got a tasty coffee or not. Finally, we have to compare the two. That's the reward prediction error. So I need the prediction, I need the outcome, and I need the comparison to generate the reward prediction error.

What are the neural systems involved? There isn't a simple answer, but evidence suggests that a lot of the frontal lobes, especially the orbital frontal lobes, are important for long-term memory, or at least having access to our memories of the values of things (Fig. 4). That may also be tied up with an intersection of goals and memory systems. If we said the orbital frontal cortex has a big role in the value, then it's going to be our sensory systems that are going to give us information about the feedback: the taste of coffee, the sound of the music I hear, or the experience I have when I try to hit a baseball. That feedback can come from very different systems depending on what kind of reward we're talking about. The activity level of dopamine neurons is, in a sense, best described as a reward prediction error. It used to be thought that dopamine was for reward only. Rats would press levers to get dopamine even if they'd starve to death, so it was thought that dopamine was a reward reinforcement signal. The subtle difference is that rather than just the reward signal, it's actually more about the reward prediction error. So if I expect tasty coffee and I get a tasty cup of coffee, that's a good thing, but I don't get much of a reward signal. I don't really get a strong dopamine signal because there was no error. I got the reward that I expected. It's not a negative prediction error signal, but it doesn't strengthen things.

BSJ: Could you briefly describe what multi-armed bandit tasks and button-press tasks are? What is the distinction between execution failure and selection error, and how did you modify the setup of the classic 2-arm bandit task to distinguish between the two?

RI: To study human behavior, one of the things that economists like to do is to set up probabilistic reward tests. The bandit tasks come from the idea of slot machines, which are frequently called one-armed bandits because they're stealing your money. Classic behavioral economics experiments present three different slot machines, but the experimenter controls the payoff and probability for each of those three machines, which change over time. If I'm smart, I'm always going to go to the machine with big payoffs and big probabilities because I have greater expected value. I might choose a slot machine with big payoffs but low probabilities, or one with little payoffs but big probabilities. Then it's a matter of whether the person is risk-seeking or cautious.

But in the classic way that these studies have been done, you just press buttons and there are no reward errors. We basically repeat that, but we now make people reach out and touch the bandit. They don't have to pull the slot machine, but they have to reach out, because if you're just pressing the buttons, there isn't any action or execution error. We're making a more realistic situation. Actually, this project got started partly by us watching big ospreys on the east coast. An osprey is like an eagle, but it's a seabird. It swoops around and then suddenly, it does a dramatic dive. From my informal observations, the osprey's hit rate is maybe about 25%, so it's diving a lot but coming up with no fish. It can't be all that pleasant to slam your face into the water. So the osprey has to make a decision. It wants that fish, it values it, and it has to make the right choice. Then, it has to make a perfectly timed dive. Afterwards, the osprey has to figure out, "Did I actually dive at the right thing, and I just missed because I didn't dive well? Or was I diving at something that didn't really exist?" The latter question is a choice problem. The osprey has to decide: "Did I really make the right choice to think that that little flash I saw was a fish?" And then another problem: "If it was a fish, then what did I do wrong in my motor system that I can learn from to do better in the future?" So that's why we thought it was important to bring in the action component to these choices. How do you decide if it was a problem of choice (selection error) or a problem of execution (execution failure)? It's a fundamental distinction we always have to make.

BSJ: What is functional magnetic resonance imaging (fMRI), and what are its applications in cognitive neuroscience?

RI: Well, fMRI has definitely taken over cognitive neuroscience. An MRI is a way to get a picture of internal anatomical structures. It takes advantage of the fact that the body is composed of a lot of water, and molecules can be made to vibrate at certain frequencies by exposing them to a magnetic field. That allows you to get these beautiful pictures of the structure of the body. We take an MRI scan to look for things like tumors. Functional MRI (fMRI) resulted from the insight that as parts of the brain are active, their demands for oxygenation change because they use up the oxygen and they have to be resupplied. The molecules in oxygenated versus deoxygenated blood are different. So we can then set up a magnetic field to perturb those molecules and then measure the signals emitted when we remove that magnetic field. Basically, it's an indirect way to measure how oxygen is being utilized in the brain, or how blood supply is being distributed in the brain. We're only measuring metabolism, not neurons. But we make inferences because we know that the parts of the brain that are more active are going to require more blood.

BSJ: Through fMRI, you demonstrated how specific brain regions respond to the distinct types of failure we previously discussed. How do neural signatures differ for execution versus selection failures, and what is the significance of these differences?

RI: There's literature from doing standard button bandit tests in the fMRI scanner which shows that when people play the slot machine and get a big payoff, there is a big positive reward prediction error in the dopaminergic parts of the brain, implicating those regions in reward prediction error. So if I don't get that reward, but it's because of an execution error rather than a reward prediction error, do I still see that dopaminergic signal?

When I don't get the payoff from the slot machine because of an execution error—say I didn't pull the slot machine arm properly—we don't see much of a reward prediction error or the corresponding dopamine signal. These results suggest that the reward system has input from the motor execution system.

BSJ: You are on the editorial board for *Cerebellum*, and you have been an editor for many scientific journals in the past. What do you foresee for the future of scientific publication?

RI: There's a financial challenge because everyone wants everything to be available online and open access. But then how do you pay for the costs of the publication process? Of course, there are people who say that we shouldn't have the publication process anymore, we should just post the articles and then word of mouth will help spread the good ones, that we should just let natural selection operate and get rid of the journals entirely. Others think that the journals serve a useful purpose by facilitating the peer review process, by having some insiders evaluate the merits of the paper. But again, people also think, "Why should we allow two or three reviewers to have such power over whether something gets published or not?" So journals are experimenting with different techniques.

I'm actually one of the editors at *eLife*, [a peer-reviewed, open access journal]. One of the papers we talked about in this interview was published through a new experiment at *eLife*. We send them the paper, and they look it over and decide whether it's worthy of review. Then, if they invite you to have it reviewed, they have a policy where the reviewers don't decide whether it's published, but the authors do. That's pretty radical. So we get the feedback, and we then decide how we want to change the paper in response. We could publish the paper as it is or retract the paper. Or, we could modify the paper and say we'd like the reviewers to comment a second time. So you can see both the author's view along with some commentaries on the value of the paper. I think more experiments like this are going to come along because there is a fundamental question: should editors and a very small number of reviewers be making the big decisions about publication, or should there be a way to actually get all the information about the process out there?

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