Learning active sensing strategies using a sensory brain–machine interface

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Diverse organisms, from insects to humans, actively seek out sensory information that best informs goal-directed actions. Efficient active sensing requires congruity between sensor properties and motor strategies, as typically honed through evolution. However, it has been difficult to study whether active sensing strategies are also modified with experience. Here, we used a sensory brain–machine interface paradigm, permitting both free behavior and experimental manipulation of sensory feedback, to study learning of active sensing strategies. Rats performed a searching task in a water maze in which the only task-relevant sensory feedback was provided by intracortical microstimulation (ICMS) encoding egocentric bearing to the hidden goal location. The rats learned to use the artificial goal direction sense to find the platform with the same proficiency as natural vision. Manipulation of the acuity of the ICMS feedback revealed distinct search strategy adaptations. Using an optimization model, the different strategies were found to minimize the effort required to extract the most salient task-relevant information. The results demonstrate that animals can adjust motor strategies to match novel sensor properties for efficient goal-directed behavior.

intracortical microstimulation | water maze | rodent

Perception is an active process. Animal behaviors are replete with examples. Active sensing is not merely the exploratory movement of sensors, but instead a purposeful motor strategy to extract task-relevant sensory information, given the characteristics and constraints of the sensors (1). Common examples of active sensing include echolocation in bats (2), electrolocation in fish (3), vibrissal touch in rodents (4), and visual search in humans (5). The observed strategies are task dependent (6) and accompanied by tailored neural processing of the sensory signals (7, 8).

However, little is known about how active sensing strategies may be modified through experience (1). The acquisition of new motor skills is known to be accompanied by reciprocal plasticity in sensory and motor areas and changes in sensory perception (9). Modified strategies may also arise after neurological conditions that impair sensory or motor capabilities (10), and in subsequent use of assistive technologies. For example, such learning could be important for users of neuroprostheses that replace lesioned sensorimotor pathways with artificial ones through a brain–machine interface (BMI) (11, 12). Studying learning in this domain could reveal both the capacity for achieving new motor strategies to optimally extract sensory information and the cost functions that drive the process.

How do we effectively study learning of active sensing strategies? First, we require a closed-loop paradigm whereby task-relevant sensory information is experimentally manipulated during free behavior (13). Second, the paradigm should be parametrically controlled to show that different sensor properties result in different motor strategies (14). Finally, theoretical optimal behaviors for the different sensor properties should ideally be known to compare to the observed behaviors (14). Virtual reality paradigms provide an option to meet these objectives,

as demonstrated recently in weakly electric fish (15). However, in general, virtual reality is difficult to implement in unrestrained animals (16). As an alternative, we propose that the same BMI technology developed for clinical purposes can provide an experimental platform to study learning during free behavior.

Motor BMIs, which decode neural activity to control an effector, have previously been used to study fundamental aspects of procedural learning (17–19). The closed-loop paradigm involves experimentally manipulating a learned decoder (*SI Appendix*, Fig. S1A) and observing how the resulting task errors, perceived naturally by the subject, drive improved performance and reorganization of the decoded neural network (20, 21). For learning active sensing strategies, we propose an analogous paradigm using sensory BMIs, which encode sensory information with direct neural stimulation (11). In this closed-loop paradigm, the encoder provides task-critical sensory information that is dependent on natural movements but that is not available to the natural senses. The encoder is then parametrically manipulated, for example, by specifying a new encoding function or brain site, and the resulting performance and behavioral strategies are assessed (*SI Appendix*, Fig. S1B).

Here, we used this experimental paradigm to study active sensing strategies in freely behaving rats performing open-field navigation to a hidden goal location. The closed-loop sensory BMI provided the only task-relevant information, egocentric bearing to the goal, with varying degrees of acuity. We found that the rats learned to use the artificial feedback to reliably find the goal, using distinct searching strategies that optimally identified the task-relevant information.

Significance

Our sensory experience is governed by sensor properties (e.g., eye photoreceptors) and corresponding motor strategies to sample the environment (e.g., eye movements). With injury, aging, or new task constraints, existing strategies can become incompatible with perceptual demands. Using a brain–machine interface paradigm in rats, we studied how motor strategies are adapted to new sensory inputs to accomplish a difficult searching task. We show that the strategies can be dynamically regulated through experience to optimally extract task-relevant sensory information.

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Fig. 4. Strategies for using the ICMS feedback. (A) Illustration of how a ICMS transition (off-to-on) could be used to identify the goal-direction vector (blue arrow) for $\sigma = 90^\circ$, $\mu = 180^\circ$. (B) Actual trial (rat Ro, $\sigma = 90^\circ$, $\mu = 180^\circ$) demonstrating the goal direction lines (blue) at σ° from the heading at each ICMS (red) transition. (C) Typical examples of actual swim paths for $\sigma = 90^\circ$ for 3 rats. (D) Typical examples of actual swim paths for $\sigma = 45^\circ$ (rats Fr, Ca) or $\sigma = 15^\circ$ (rat Ge). (E) Total curvature of the swim path (mean $\pm$ 95% c.i.) for postlearning trials of each rat.

angle $\varphi = 90^\circ$ from the instantaneous swim path at the ICMS off-to-on and on-to-off points are shown in blue. With this initial information, the rat then swam generally toward the platform, but with a clear deviation from the true direction. Then, a second ICMS train occurred, prompting a corrective loop leading closer to the platform. Finally, the rat overshoots, receives a third ICMS train, and makes a final turn to reach the platform. A similar strategy was observed across all the rats that learned the $\sigma = 90^\circ$ condition (e.g., [Movies S7](#) and [S8](#)). In particular, the rats swam in a spiral or circular pattern in the middle of the tank to efficiently gather initial ICMS feedback, followed by a swim toward the platform with a tight corrective loop if ICMS was encountered again (Fig. 4C).

In contrast, in the $\sigma = 45^\circ$ and 15° conditions, the rats adopted a very different strategy. The swim paths almost entirely lacked any tight spiraling or looping. Instead, often a zigzagging strategy

was used in which side-to-side movements generated ICMS transitions, presumably to better define the goal direction (Fig. 4D). A similar strategy has been observed in rats following a wide odor trail (28). To quantify the difference in looping versus zigzagging swim trajectories, we computed the total curvature of the swim path (i.e., the sum of the rat's yaw rotation between each pair of consecutive frames) for each postlearning trial. The mean total curvature was significantly higher in the 4 rats that learned to use low-acuity feedback than in the 3 rats that learned to use high-acuity feedback (Fig. 4E; $t[5] = 5.74$; $P = 0.0022$). Importantly, there was no mean performance difference, quantified by path length ratio, between these same groups ($t[5] = 0.002$; $P = 0.9984$). Thus, with equivalent performance, the characteristics of the encoded sensory information caused distinct motor strategies to be learned.

Search Strategies Minimized Effort Needed to Identify ICMS Transitions. Finally, we asked why these different strategies might be appropriate for the encoded directional sense. As just described, the encoding function edges, or ICMS transitions, provided the most information for goal localization. From the point of view of mechanics, looping and zigzagging might minimize the torque needed to rotate in the water to find the edges of wide and narrow encoding functions, respectively. To explore this hypothesis, we considered a simple model of yaw rotation dynamics: $\tau = I d^2 \theta / dt^2 + b d \theta / dt$, where $\tau(t)$ was the control torque, $\theta(t)$ was the heading (goal-direction) angle, I was the yaw axis moment of inertia, and b was the coefficient of frictional resistance (or drag) in water. Using Pontryagin’s minimum principle, we derived optimal solutions to control the heading trajectory from an initial condition of $\theta(0) = 0^\circ$, to $\theta(t_1) = \sigma$ (first edge), and then to $\theta(T) = -\sigma$ or $2\pi - \sigma$ (second edge, zigzagging or looping; *SI Appendix*). We also left as a free parameter the angular speed, ρ , at $t = t_1$ and $t = T$. The optimal time of first edge interception, t_1^* , optimal heading, $\theta^*(t)$, and optimal control torque, $\tau^*(t)$, were determined separately for the zigzagging and looping terminal constraints. We then compared the total effort (i.e., integrated squared torque) used by zigzagging and looping to determine which strategy was optimal over a range of model parameters (*SI Appendix*).

Two examples are shown in Fig. 5A. Using estimates of l and b based on the rats' body morphology, we found that it was more efficient to zigzag than to loop when $\sigma = 45^\circ$, in agreement with the rats' learned behavior (Fig. 5A, *Left*). For the same parameters, when the encoding function was widened to $\sigma = 75^\circ$, it was optimal to loop rather than zigzag (Fig. 5A, *Right*). In general, the optimal strategy for a given σ was dependent on the ratio b/l and ρ (Fig. 5B). Over the range of parameters tested, it was always optimal to loop at $\sigma = 90^\circ$. For $\sigma < 90^\circ$, zigzagging became optimal at slower angular speeds or if drag relative to inertia became large. At $\sigma < 50^\circ$, it was always optimal to zigzag (Fig. 5B). Thus, this simple mathematical model and hypothesized cost function produced results that were in general agreement with the observed search strategies used by the rats. Furthermore, the model predicts that we should observe looping behaviors at $50^\circ < \sigma < 90^\circ$, provided the angular speeds used by the rats are sufficiently high.

Discussion

The majority of sensory BMI studies have focused on the detection and discrimination of ICMS in the absence of information-seeking movement (i.e., passive sensing) (11, 24, 25, 29). The relatively few active sensing BMI studies to date have used searching tasks, where the goal is recognizable (e.g., by external reward), but its location is found only through interpretation of ICMS feedback or by random search. In these searching tasks, 2 types of feedback have been tested: goal contact and goal direction. In the contact paradigm, ICMS is delivered when a natural or neuroprosthetic effector spatially overlaps the goal (30–32). This feedback is analogous to tactile signals arising from contact with an object. Therefore, the paradigm is informative to

Fig. 5. Modeling optimal search strategies. (A) Optimal heading trajectory, $\theta^*(t)$, to identify edges of an encoding function with width of $\sigma = 45^\circ$ (Left) or $\sigma = 75^\circ$ (Right), using a zigzagging strategy (gray) and a looping strategy (red). Model parameters were $l = 6.5 \times 10^{-4} \text{ N}\cdot\text{m}\cdot\text{s}^2$, $b = 1.5 \times 10^{-5} \text{ N}\cdot\text{m}\cdot\text{s}$, $\rho = 200^\circ/\text{s}$, and $T = 0.8 \text{ s}$. The optimal time to first edge (t_1^*) and integrated squared torque (effort) are indicated for each strategy. Illustrations of the model rat's heading using the minimum effort strategy are indicated at the top for 4 points along the trajectory. (B) Model predictions of the optimal strategy over a range of parameters and $T = 0.7 \text{ s}$.

an artificial sense of touch for neuroprostheses. However, for the study of active sensing, the paradigm is limited, since the motor strategy to search for the goal is independent of ICMS until the point at which it is encountered. In the direction paradigm, ICMS provides feedback about the goal direction, which is noncontact spatial information analogous to natural vision or audition rather than touch, and which is naturally encoded in entorhinal-hippocampal circuits (33, 34). This paradigm affords the subject an opportunity to tailor their motor behavior to the ICMS feedback properties to efficiently search for the goal. Prior work has shown that rats can learn to discriminate between 4 potential goal locations on the basis of ICMS delivered when their heading coincides with the direction of the true goal location (35). Several variations on this result were subsequently reported (26, 36, 37).

Our sensory BMI experiment also used a searching task with goal direction feedback. However, several features distinguish our study from prior ones. First, we parametrically varied the encoding function to directly explore whether and how searching strategies varied with feedback properties. Specifically, we tested the full range of the parameter specifying acuity of the artificial sense. Performance and goal direction acuity had a U-shaped relationship, which we interpreted as resulting from a decrease in ICMS detectability at higher acuities. This tradeoff might be circumvented by mimicking natural sensory adaptation (38), with intensity starting high enough for short bouts of ICMS to be detected and gradually decreasing such that longer episodes remain perceivable while minimizing charge injection. Importantly, we also observed different learned active sensing strategies: looping for low-acuity feedback and zigzagging for high-acuity feedback. Prior studies investigated reversal learning by changing the encoding function, but only at the level of performance (26, 36). Second, we identified an optimal strategy as a function of the encoding parameters, which involved precise turning at ICMS transitions. The swim paths indicated that ICMS transitions were indeed exploited. Our model indicated that the learned strategies were optimal for encountering these transitions. Third, we used a continuous-location searching task, implemented in a water maze to provide intrinsic goal-seeking motivation (23). The task was significantly more challenging, requiring many more trials to learn, than prior discrete-location tasks. Impressively, the rats learned to use ICMS to locate the randomly located hidden platform with the same proficiency as natural vision.

Together, these features establish sensory BMI as a platform for studying learning of active sensing strategies. Much of the active sensing literature is devoted to elucidating the elegant

solutions, refined through evolution, that model organisms use to enhance sensory information through movement (39, 40). Solutions are often hard-coded in the body plan and movement abilities of the animal, distribution of sensory receptors, and tuning of primary sensory neurons. However, changes in neural response properties, neural functional connectivity, and attentional sampling could allow active sensing routines to be shaped through experience (41). An important line of inquiry is to investigate how active sensing strategies are dynamically regulated or adapted to changes in an organism's sensorimotor apparatus or ecological niche (13). Sensory BMI, compared with virtual reality, is more compatible with studying learning during free behavior. A potential disadvantage is the nonethological nature of the stimuli. Thus, the sensory BMI method is particularly well suited to studying active sensing adaptations to pathological or unnatural sensorimotor contingencies, such as occurs with neurological injury and neuroprosthetic treatments. As exemplified by our work, such studies can reveal the animal's learning capacity in this domain, the explicit relationship between sensor properties and sensing strategies, and how the strategies compare to known optimal alternatives.

Methods

Surgery. The following procedures were approved by the University of Pennsylvania Institutional Animal Care and Use Committee. Sprague-Dawley rats ($n = 12$; male; initial weight 250–275 g) were purchased from Charles River Laboratories. Before surgery, the rats were habituated to handling for approximately 1 wk. Then, an aseptic surgical procedure was performed to implant a concentric bipolar stimulating electrode (MS308, Plastics One), with 150- μm inner electrode diameter and 1-mm interelectrode distance, into a target cortical area. The rats were given preemptive analgesia (buprenorphine SR, 1.2 mg/kg) and anesthetized with an i.p. injection of ketamine (60 mg/kg) and dexmedetomidine (0.25 mg/kg). Once placed in a stereotaxic frame, a 2-mm-diameter craniectomy was performed and the electrode was slowly advanced into either S1 or A1 (coordinates in *SI Appendix*, Fig. S4). Dental acrylic was applied to form a permanent headcap around the electrode and skull screws. The rats were given 7 d after surgery to recover before training resumed.

Training. After recovery from surgery, the rats were reintroduced to handling and habituated to wearing a harness to which a wireless neural stimulator was attached (Fig. 1A). Then, they performed a visually guided search task for 3 to 7 daily sessions in a Morris water maze (23). The Morris water maze consisted of a 2-m circular metal tank with a black interior, filled with water of ambient temperature (18–22 $^\circ\text{C}$) to a depth of about 25 cm. The water was made opaque with black tempura paint to hide a 10-cm circular

acrylic platform submerged by 2 cm. On the visually guided task, a white ruler protruding 15 cm above the water was attached to the platform to provide a local visual cue of its location. On each trial, the platform was moved to a random location. Each trial began by placing the rat within a body length of the center of the tank (13.7 ± 2.3 cm from center on average across all trials and rats) and at a relatively consistent orientation (27.8° SD). The rat then swam to find the platform to escape the maze. Training concluded when the rat consistently appeared to be actively looking for the local visual cue and reaching the platform without anxious or inattentive behaviors such as clinging to or following the walls of the tank (thigmotaxis). Performance on the final 20–30 trials of the visually guided task was used to provide a baseline to which learning on the stimulation-based task was compared. All animals that completed training as described were included in the experiment ($n = 7$). Four rats were excluded due to repeated signs of stress (e.g., excess vocalization) and thigmotaxis during training that did not ameliorate over time. Per our protocol, these animals were removed from the study. An additional rat was excluded after its chronic implant detached from the head.

Experiment. After training, the local visual cue was replaced with ICMS that encoded the rats' egocentric bearing to the platform. The objective of the experiment was to see whether and how the rats learned to use this artificially encoded information. The encoding paradigm required a closed-loop system to update ICMS parameters in real-time, based on the swim path (Fig. 1B). The custom closed-loop system was described previously (22). Briefly, a video camera with a 1080p image sensor was placed above the center of the Morris water maze to monitor the rat's swim path at 12 frames/s. A computer program (MATLAB) acquired each video frame, identified the rat's heading relative to the platform, and computed ICMS parameters based on the encoding function specified by the experimenter (Fig. 1C). The rat's heading was determined by identifying, on each frame, a red landmark on the wearable stimulator corresponding to the position of the rat's upper back, and computing the orientation of the vector between the identified positions on every pair of consecutive

frames. On each video frame, the updated ICMS parameters were sent wirelessly to the neural stimulator, using a 2.4-GHz transceiver.

The wearable stimulator ($20 \times 25 \times 15$ mm, 15 g) delivered bipolar, biphasic, current-controlled pulses with programmable pulse width, pulse amplitude, and pulse frequency. For these experiments, pulse width and frequency were fixed at 0.2 ms/phase and 100 Hz, respectively. Pulse amplitude, determined at the beginning of each session, was set at the threshold for a behavioral response to 500-ms pulse trains. Current amplitude was increased until the experimenter detected a clear response (e.g., turning the head contralaterally or twitching or scratching the whisker pad) to 2 consecutive pulse trains (42). The range of pulse amplitudes used was 15 to 75 μ A. The stimulator was battery powered, encased in waterproof rubber latex, and attached to the harness via cable-tie fasteners. The stimulator transmitted back to the acquisition computer on each frame the measured voltage on the electrodes. This allowed us to track the electrode impedance throughout each trial, and to exclude trials in which large impedance changes occurred, typically due to water infiltration or loosening of the electrode connector. These events occurred on less than 3% of trials.

Experiments consisted of a series of multisession trial blocks in which different encoding functions were tested. Testing conditions for each rat are listed in *SI Appendix, Table S1*. To assess learning, the effect size (Hedges' g statistic) was computed between the path length ratio distributions of the local visual cue trials and ICMS trials in nonoverlapping 20 trial blocks. Two consecutive ICMS trial blocks with a $|g| < 0.5$ was used as the learning criterion. Catch trials, in which no ICMS was delivered, were randomly interleaved with ICMS trials in the postlearning periods to further assess reliance on the ICMS feedback. Through the use of catch trials, each rat served as its own control. At the conclusion of the study, the electrodes were localized to the target cortical areas using histology (*SI Appendix*).

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