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LÉVY WALKS EMERGING NEAR A CRITICAL POINT

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ABSTRACT

In biological movements, a special class of random walks, the so-called Lévy walk, has been widely observed. It has been shown that Lévy walks outperform normal random walks in terms of search efficiency because of rare, long, straight movements among short steps, and thus the cause of its prevalence is considered to be a consequence of natural selection. However, recent findings suggest that Lévy walks might also be the result of other mechanisms. This suggests that its origins depend on ecological and physical conditions. Although it is crucial to explore the mechanisms of producing Lévy walks by considering various conditions, the generative mechanisms of Lévy walks based on internal states with nonlinear dynamics are less understood. Here, we develop a generative model composed of simple deterministic nonlinear systems and show that the Lévy walk of an autonomous agent can emerge near the critical point, which is between the synchronous and asynchronous states. Furthermore, we show that Lévy walks have maximized sensitivity to a perturbation and can produce diverse behavior, which might be another advantage of Lévy walks. Our results suggest that the commonly observed Lévy walk can be derived from the critical point hypothesis in which biological systems sitting in a critical point between order and disorder receive benefits. This provides new insights into understandings of how and why Lévy walks are prevalent in biological systems.

Keywords Lévy walks | random search | criticality | nonlinear dynamics | autonomous agent

Introduction

Lévy walks, which are a special class of random walks with step lengths ℓ following a power law distribution $P(\ell) \sim \ell^{-\mu}$ where $\mu \in (1, 3]$ is a power law exponent, are observed in a variety of biological movements and agents, ranging from cells and insects to mammals, humans, and even memory retrievals in human cognition [1, 2, 3, 4, 5, 6, 7, 8]. Lévy walks allow agents to exhibit rare long straight movements among many short steps. This characteristic leads to more efficient searching or foraging strategies than normal random walks, so-called Brownian motion, when the targets (e.g., food, mates, or habitats) are unpredictably and scarcely distributed in the environment [9, 10, 11]. Therefore, according to the Lévy walk foraging hypothesis, evolution through natural selection can explain the fact that Lévy walks are widespread in biological movements.

However, there has been a recent debate about the origin of Lévy walks [12, 13]. While the Lévy walk foraging hypothesis can explain the prevalence of Lévy walks, as mentioned above, Lévy walk patterns can occur for other reasons, especially through interactions with a complex environment [12, 13].

For example, Lévy walks are observed in the movements of plant seeds, which are thought to result from the interactions between the turbulence of the wind and the shape of the seeds. Based on these facts, the important consideration is that the generative mechanisms for Lévy walks must be not unique but diverse [12, 13]. Therefore, it is imperative to explore the mechanisms, their consequences, and their dependence on biological and physical factors or ecological conditions for the full understanding of Lévy walks in biological movements.

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One of the candidate mechanisms of Lévy walks is the spontaneous dynamics, generated by internal states such as nervous systems. Previous studies on spontaneous behavior revealed that temporal patterns in intervals between consecutive rapid turns or rest/move without a stimuli condition often follow a power-law distribution [14, 15, 16], which is a hallmark of Lévy walks. Also, movement trajectories of some animal species in a featureless environment often corresponded to Lévy walks, suggesting that Lévy walks were generated intrinsically [17, 18, 19].

Such temporal organizations in spontaneous behavior or movement patterns in Lévy walks in some species should be based on nonlinear dynamics or chaotic dynamics [20, 14, 21, 22]. Moreover, in an ant species *T. albipennis*, there is a scaling relationship between the length of the active duration of the movement and the movement speed, suggesting that the active duration is determined in advance, and that the decision making is deterministic rather than stochastic [23, 24]. Following these facts, it is crucial to understand how nonlinear dynamics can produce Lévy walks and what advantages they confer to biological agents. However, general conditions and the consequences of Lévy walks based on dynamical systems remain less understood.

In this study, we develop a generative model composed of simple, deterministic, nonlinear systems for the movements of autonomous agents and show that various types of movements can be generated depending on parameters, which determine the attractors of systems. Then, we show that Lévy walks can emerge near a critical point between an ordered phase, whose dynamics are completely synchronized and a disordered phase, whose dynamics are asynchronous. We also show that the trajectory of agents near the critical point can become the most sensitive to perturbations. This is considered an advantage of Lévy walks for producing diversity and avoiding resource competitions. These findings could be related to a critical point hypothesis proposed in the context of brain dynamics and complex systems [25, 26] and provide novel insights into understanding of how and why Lévy walks emerge in biological systems.

Results

Movements obtained from the model

We modeled movements of autonomous agents (e.g., animal individuals) based on their internal states. Given that nonlinear systems underlie brain dynamics [14] and Lévy walks as well [21], it is reasonable to construct a minimal model composed of a few (here: two) nonlinear oscillators as internal states , x_t and y_t, of the agents (see Methods), as pointed out by [27]. In particular, as the signature of chaos has been found in movements and neuronal firings [21, 28], we set the nonlinear function of the model as the dynamics to be chaotic (here, a tent map). Moreover, connections between elements are ubiquitous in biological systems [29], and thus the model has a parameter $\varepsilon \in [0, 0.5]$ that describes the coupling (connection) strength of elements in the system. We consider the motor outputs from the dynamics, x_t and y_t (Fig. 1A). For simplicity, while the movement speed is kept constant, the movement is generated from the turning angle $\Delta\theta_t = c(x_t - y_t)$ of the movements at each time t (Fig. 1A) where c is a constant for connecting internal dynamics and outputs (see Methods). Note that we do not assume any distribution of step lengths in the movements and turning angles.

First, we show some examples of movement trajectories of agents obtained from the model and the dependency of the control parameter ε (Fig. 1B-D). When $\varepsilon = 0.1$, namely the components of the systems weakly interact with each other, the movement is similar to Brownian motions (Fig. 1B). This is because the two chaotic oscillators have less influence on each other, and the turning angle can randomly fluctuate as if they were independent random numbers. In contrast, when $\varepsilon = 0.3$, the movement is completely ballistic, namely, a straight line (Fig. 1D), because the two oscillators are completely synchronized as $x_t = y_t$ due to the strong interaction strength, although x_t and y_t fluctuate in the same manner. For an intermediate level of interaction strength, here $\varepsilon = 0.22$, we can see that the movement is composed of rare long straight movements among many short step lengths, which are characteristic of Lévy walks (Fig. 1C). An illustration of the internal dynamics and the attractors corresponding to the movements makes it possible to intuitively grasp the mechanisms for producing such movements (insets of Fig. 1B-D and Fig. S1). Note that $\Delta\theta_t$ in the insets of Fig. 1B-D is proportional to $x_t - y_t$, and thus $\Delta\theta_t = 0$ means that x_t and y_t synchronize with each other. The internal dynamics producing the Lévy walk-like movements exhibit bursty patterns (inset of Fig. 1C), while the dynamics were always noisy for small ε (inset of Fig. 1B) and were constantly zero for large ε (inset of Fig. 1D). These results indicate that the various movement patterns stem from synchronous and asynchronous dynamics of the internal states.

To statistically verify whether these movement trajectories can be classified as Lévy walks, we fitted the truncated power law distribution and the exponential distribution to the step length distributions obtained from the modeled trajectories. A rigorous method based on the model selection that has been applied to empirical data analysis on animal movements was used for our fitting procedure (see Material and Methods) [30, 31, 32]. The example of the statistical result for a certain trajectory for $\varepsilon = 0.22$ shows that the step length distribution was judged to be the truncated power law distribution with $\mu = 1.63$ (Fig. 2B), which means the movement is classified as a Lévy walk. In contrast, the step length distribution for $\varepsilon = 0.1$ was judged to be an exponential distribution (Fig. 2B), which means that the movements

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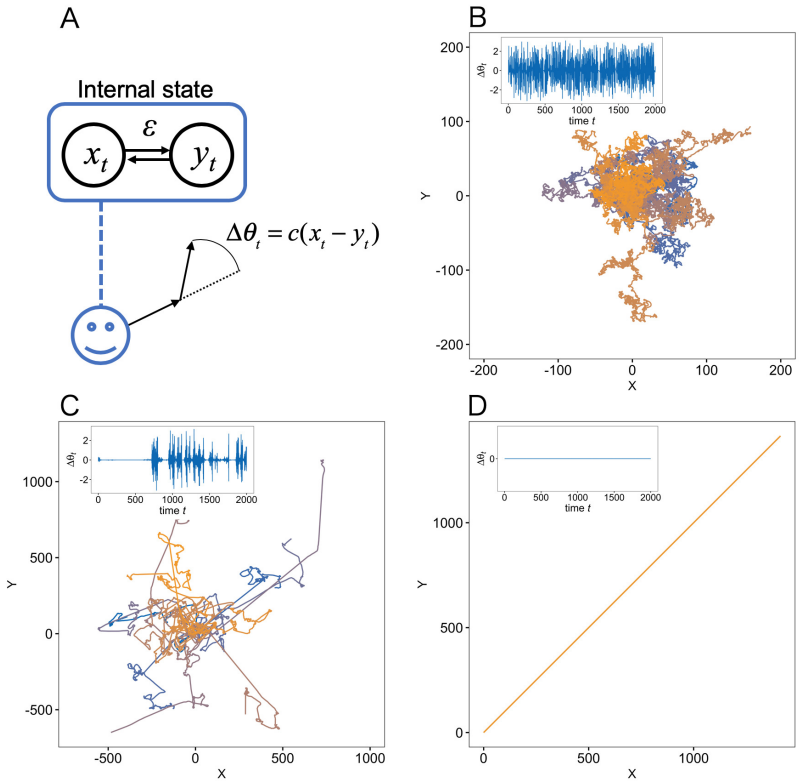

Figure 1: Our model scheme and examples of trajectories obtained from the model. (A) The internal dynamics x_t and y_t produce the agent movements. The model has a parameter determining the coupling strength between elements in the system. The movement is simply produced by turning angles $\Delta\theta_t$. (B-D) The trajectory of the agent in a 2-dimensional space from $t = 0$ to 2000 was represented by solid lines: (B) $\varepsilon = 0.1$; (C) $\varepsilon = 0.22$; (D) $\varepsilon = 0.3$. The different colors correspond to different initial conditions. Note that the trajectories in (D) are overlaid because they are exactly the same. The parameter of the tent map was set to $r = 0.7$ and the initial position $\boldsymbol{X}_0$ was set to (0, 0). Examples of the time series of the turning angle $\Delta\theta_t$ are shown in the insets. When $\Delta\theta_t$ close to zero lasts for a long time, the agent exhibits straight movement. In contrast, when $\Delta\theta_t$ fluctuates dynamically, the agent exhibits rapid turns.

are classified as Brownian motions. As there were no turns in the trajectory for $\varepsilon = 0.3$, the fitting procedure is not suitable for this data, and we manually classified it as straight movements. Also, the result of the analysis on the diffusive properties using the mean squared displacement (MSD; see details in Methods) shows that movement patterns for $\varepsilon = 0.22$ have superdiffusive characteristics, while the movement for $\varepsilon = 0.1$ has a normal diffusive characteristic (Fig. S2), which also supports that movement patterns for $\varepsilon = 0.1$ and $\varepsilon = 0.22$ are Brownian walks and Lévy walks, respectively.

Phase diagram

Then, to elucidate the conditions that are needed for the emergence of Lévy walks in our model, we draw a phase diagram (Fig. 3) by changing the control parameter ε and evaluating the internal dynamics and movement patterns. The trajectories for the same parameter set were generated by different initial conditions x_0 and y_0 (100 replicates). To characterize the internal dynamics, the order parameter of the system was calculated as the standard deviation of distributions of $\Delta\theta$ averaged over 100 replicates. Fig. 3 shows that the order parameter drastically changes from positive standard deviations to zero standard deviations for $\varepsilon \approx 0.23$, suggesting that the system exhibits a phase transition. This is also a critical point at which the synchronized state $x_t = y_t$ changes from an unstable state to a stable one with increasing ε, which can be characterized by the linear stability of $x_t - y_t$ (see Supplementary Information).

We also conducted a classification of the movements obtained with different ε and initial conditions using the statistical techniques as well as the above section. The result shows that the region of emergence of Lévy walks is poised near the critical point between the synchronous and the asynchronous phase, which corresponds to straight movements and Brownian motions, respectively (Fig. 3). At $\varepsilon = 0.22$, the ratio of Lévy walks was maximized, and the estimated

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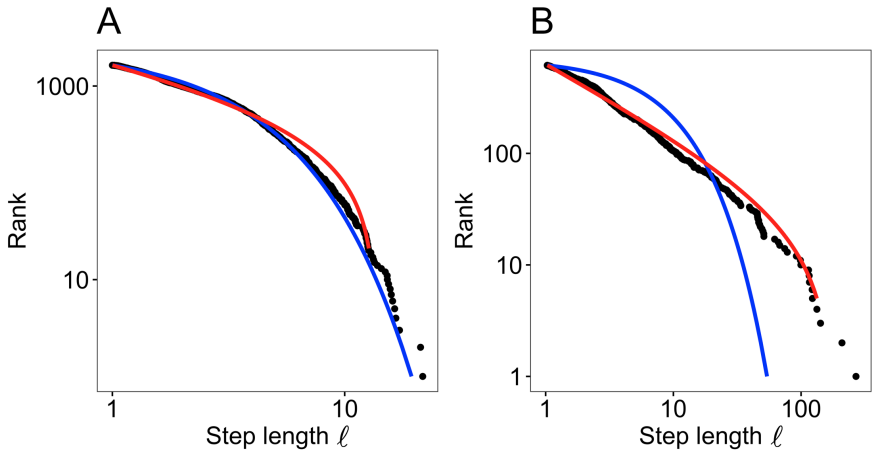

Figure 2: Log-log plot for the rank distribution of step lengths ℓ in the trajectories obtained from the model with specified initial conditions x_0, y_0. Black dots represent the step length distribution from the model movements shown in Fig. 1, with the parameters $\varepsilon = 0.1$ (A), and $\varepsilon = 0.22$ (B). The other parameters were set to $r = 0.7$ and $t_{\max} = 10000$. The red and blue lines represent the fitted distribution of the truncated power-law and the exponential distribution, respectively.

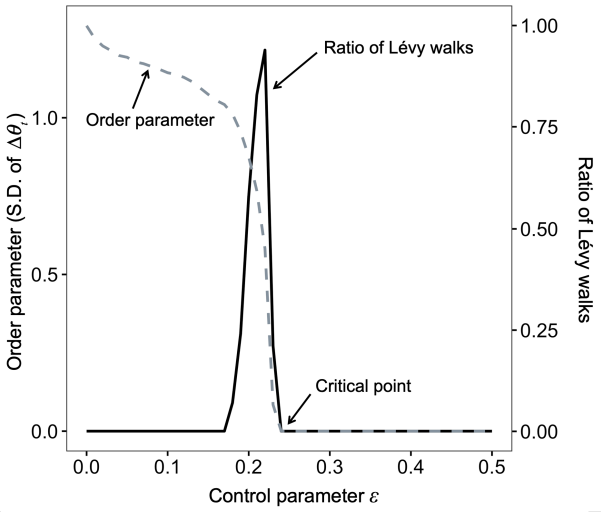

Figure 3: Phase diagram with a changing control parameter ε. The gray dashed line represents the order parameter, that is the standard deviation of the distribution of $\Delta\theta_t$. Near $\varepsilon = 0.22$ the order parameter drastically changes. The solid black line represents the ratio of the judgements of Lévy walks obtained by fitting distributions to the simulated 100 trajectories for the same parameter set. The other parameters were set to $r = 0.7$ and $t_{\max} = 10000$.

power law exponent was 1.55 ± 0.06 (mean$\pm$S.D.). As the search efficiency depends on the step length distribution and the diffusiveness [9, 10], Lévy walkers developed by our model also receive the benefits of a higher search efficiency when the targets are distributed scarcely and patchily. In addition, it is worth noting that the trajectories can change depending on the initial internal states, x_0 and y_0, while keeping the characteristics of the movement patterns mostly in the parameter range (Fig. 1B-D and Fig. S3). This can explain the variability that is often observed in animal decision making [14, 33].

Moreover, we confirmed that the emergence of Lévy walks near a criticality can be seen in other models, including a model based on different r or logistic maps (i.e., different f) (Figs. S4 and S5) [34], global coupled maps (i.e., many components) (Fig. S6) [35], and noise-additive models (Fig. S7).

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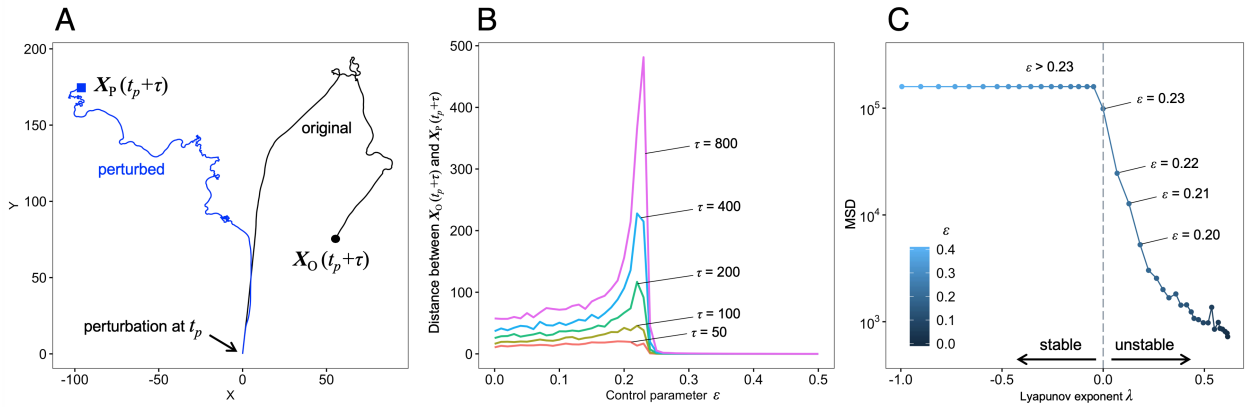

Figure 4: Sensitivity of movements to perturbations. (A) An example of trajectories for $\varepsilon = 0.22$ with (blue line) and without (black line) perturbations. We added a perturbation $\Delta x = 1.0 \times 10^{-4}$ and $\Delta y = -1.0 \times 10^{-4}$ to the internal dynamics x and y only at t_p and $\boldsymbol{X}_{t_p} = (0, 0)$. The black circle and blue square represent the position at $t = t_p + \tau$ (here $\tau = 400$) of the original and perturbed trajectories, respectively. (B) The sensitivity to perturbation changes depending on the control parameter ε. The vertical axis represents the sensitivity, namely the averaged distance between the original and perturbed trajectories at $t_p + \tau$. For example, it corresponds to the distance between the black circle and the blue square in (A) for $\tau = 400$. (C) A trade-off relationship between the instability index (Lyapunov exponent λ) of $x_t - y_t$ and the diffusiveness (MSD) of the agents. The MSD was calculated for $t = 400$. The color of the plots represents the control parameter ε. Note that the results for $\varepsilon > 0.4$ are not shown for improving the visibility. The gray dashed line denotes that the Lyapunov exponent is 0, which signifies a boundary between the stable and unstable phases.

Sensitivity to perturbations

If nonlinear dynamics, especially coupled oscillators, can produce movements observed in biological agents, is there an advantage to exhibiting Lévy walks near the critical point except for searching efficiency? We hypothesized that Lévy walks can maximize the sensitivity to a perturbation or to an input from the environment, in terms of movements, because the critical point hypothesis claims that complex systems at a critical point gain several merits, including higher sensitivity to environmental information [25, 26]. To investigate the sensitivity of the movements, namely how different the perturbed trajectory is from the original one, we introduced a perturbation into the internal states of the agents as follows: a small perturbation $\Delta x = 1.0 \times 10^{-4}$ and $\Delta y = -1.0 \times 10^{-4}$ was added to the internal dynamics x_t and y_t, only at $t = t_p$. This perturbation is a vector of the same direction with $x - y$. Then, we observed the original trajectory $\boldsymbol{X}_{\mathrm{O}}$ (i.e., without perturbation) and the perturbed one $\boldsymbol{X}_{\mathrm{P}}$, and compared them after τ time steps, i.e., at $t = t_p + \tau$. If the signal from the environment affects the internal states, the perturbation can be considered to be an input from the environment through a sensor [36]. Fig. 4A shows an example for $\varepsilon = 0.22$, in which the difference between the two positions of $\boldsymbol{X}_{\mathrm{O}}(t_p + \tau)$ and $\boldsymbol{X}_{\mathrm{P}}(t_p + \tau)$ increased with time, and finally they exhibited completely different trajectories. Here, we call the distance between $\boldsymbol{X}_{\mathrm{O}}(t_p + \tau)$ and $\boldsymbol{X}_{\mathrm{P}}(t_p + \tau)$ the sensitivity to the perturbation. An exhaustive evaluation of the sensitivity of the trajectory to the perturbation shows that the sensitivity was maximized near the critical point $\varepsilon \simeq 0.23$ (Fig. 4B) for most τ, suggesting that Lévy walks emerging near the critical point obtain a maximized sensitivity to the perturbation under our assumption that the mechanisms are based on coupled oscillators.

Then, to reveal why the sensitivity was maximized near the critical point, we analyzed the relationship between the diffusiveness (i.e., MSD) and the instability of the trajectories, which were evaluated by a Lyapunov exponent λ of $x_t - y_t$. Fig. 4C shows the trade-off relationship between diffusiveness and instability, that is, the diffusiveness decreases with increasing instability. In particular, if λ is smaller than 0, the trajectory converges to a straight line for $t \to \infty$, because the added perturbation disappears due to the negative eigenvalue. Therefore, the trajectory is less likely to change. In contrast, if λ is larger than 0, the perturbation can change the trajectory easily. However, the diffusiveness is low, which can lead to less exploration of new locations. A small positive Lyapunov exponent λ makes both instability and a high diffusiveness possible. Hence, Lévy walks emerging near the critical point can exploit maximized sensitivity owing to a combination of high diffusiveness and small instability.

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Discussion

In the present study, we tackled the problem of how Lévy walks, which are widely observed in various biological movements [1], can be produced by simple nonlinear systems. We show that Lévy walk patterns emerge near a critical point between synchronous and asynchronous states (Figs. 1-3). Generative models in previous studies on Lévy walks can be classified into two types: based on interaction with environments and based on internal states. Although the former model can explain some cases of Lévy walks observed in biological movements [13], the empirical evidence for intrinsically motivated Lévy walks has accumulated [17, 18, 19]. Theoretical studies on search efficiency have implicitly assumed that the movement patterns are caused by intrinsic mechanisms. However, they have focused only on the probability distribution of the step lengths and turning angles, and thus have ignored the generative mechanisms for intrinsic movements [9, 10, 11]. When one tries to fully understand why Lévy walks are widely observed in biological systems, it is essential to explore how the brain or systems related to behavior can produce Lévy walks intrinsically [27, 22, 37, 38]. Here, we assumed the simplest deterministic nonlinear model for intrinsic movements. Nevertheless, the produced movement patterns were complex enough and varied from Brownian walks to Lévy walks and ballistic movements depending on the parameters (Fig. 1). This reflects the synchronous and asynchronous dynamics in internal states which are ubiquitous in the brain [29]. While animals with high cognitive ability may adopt Lévy walks based on rational decision-making [37], it is reasonable that those with low cognitive ability, such as insects, adopt a simpler mechanism comprising of nonlinear chaotic oscillators. It is worth noting that only one parameter is required for controlling movement patterns in our model, suggesting that it is easier to obtain and maintain Lévy walks through natural selection, as compared to other mechanisms with many parameters.

In our model, the coupling strength of the system can drastically alter movement patterns (Figs. 1-3). Theoretical studies have shown that the optimal searching strategy can change depending on the ecological context, such as density of targets, risk of predation, and kinds of objects being searched [39, 40, 41, 42]. Some empirical studies have reported that animals do not always exhibit Lévy walks [4, 5, 3]. Therefore, it is possible that the plasticity in spontaneous behavior caused by changing the coupling strength of the systems can lead to adaptive responses to environmental conditions. Moreover, differences in movement patterns can also impact not only the fitness of the agent but also higher systems, such as epidemic dynamics and ecosystems through interactions with other agents. For instance, Lévy walks allow more resilient prey-predator systems than normal diffusion movements would in degraded conditions [43]. Therefore, understanding the mechanisms and controllability of Lévy walks can lead to predicting and controlling the consequences in higher systems.

So far, the main advantage of Lévy walks has been considered to be its high search efficiency [1, 11, 12]. However, optimal foraging should not be the only evolutionary force in favor of Lévy walks [12]. Our result suggests that Lévy walks near the critical point outperform Brownian walks and ballistic movements within the model in terms of not only search efficiency but also sensitivity to perturbations (Fig. 4). For example, it may correspond to the situation that Lévy walks strategy can avoid resource competition among conspecific individuals under a certain resource distribution. In other examples, producing diversity in movement trajectories can lead to discovering new resourses or options. Most importantly, by assuming the mechanisms of producing movement patterns, we found a trade-off relationship between diffusiveness and instability (Fig. 4C). As such constraints for biological agents yield different fitness landscapes, we can find the benefits of a certain movement pattern, which is the higher sensitivity of Lévy walks under the trade-off, which suggests that considering biological mechanisms provides novel insights into the understanding of the evolution of movement patterns.

In the context of brain dynamics and complex systems, a critical point hypothesis has been proposed [25, 44, 26, 45, 46, 47]. It claims that systems sitting at or near a critical point between order and disorder states have various functional advantages ranging from adaptive responses to the fluctuated environment to the production of various scale behavior and computational abilities [26, 44, 48]. Therefore, it is reasonable that various biological systems, including brains, gene regulatory networks, and cell and animal groups exhibiting collective motions carry the signature of being near a critical point [25, 26, 45, 46]. Likewise, in our model, agents with internal states near the criticality between stable synchronous states (i.e., order) and chaotic asynchronous states (i.e., disorder) exhibit Lévy walks, which benefit from a high search efficiency and high sensitivity, as shown in this study. The high search efficiency is a result of the large variance in step length distributions (Fig. 2B), that is, generating short to long step lengths, which can be classified as an advantage in large repertoires of behavior [26]. The high sensitivity comes from the characteristics of flexibility and robustness. The flexibility needs a positive Lyapunov exponent of the system, while the robustness requires a small Lyapunov exponent. Therefore, a small positive Lyapunov exponent produces both the ability to change and the high diffusiveness derived from the long step length (Fig. 4C). Consequently, the differences amplified by high diffusiveness lead to different trajectories and positions (Fig. 4A and B). From these results and from the literature on critical point hypothesis, there emerges a possibility that the main evolutionary force of Lévy walks is not search efficiency. It is

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worth noting that systems near a critical point receive some kinds of benefits simultaneously, and thus Lévy walks may be widely observed in nature.

As we have proposed a model for Lévy walks, it is important to empirically explore the core network playing a role in the Lévy walk generator in the brain [49]. Experimentally changing parameters related to movement patterns, for example, neuromodulators allows us to reveal how and why animals adopt Lévy walks. Furthermore, although we have mainly focused on spontaneous behavior, it is crucial to unveil how spontaneous dynamics, sensory inputs, and motor outputs interact with each other to be able to comprehensively understand the behavior of biological autonomous agents [50].

Methods

Model

To model Lévy walks based on nonlinear dynamics, we consider an autonomous agent with internal states that are composed of a minimal neural network-like system. The system has only two elements denoted by $x_t, y_t \in [0, 1]$ and follows nonlinear dynamics with discrete time. The movement of the agent is determined by the internal states (see details below). Then, we observe the positions $\boldsymbol{X}(t) = (X_t, Y_t)$ of the agents in a continuous 2-dimensional space, and evaluate their movement trajectory.

We assume the update rules of the internal states to be the following equations:

$$x_{t+1} = (1-\varepsilon)f(x_t) + \varepsilon f(y_t) \quad (1)$$

$$y_{t+1} = (1-\varepsilon)f(y_t) + \varepsilon f(x_t) \quad (2)$$

where $\varepsilon \in [0.0, 0.5]$ is a coupling strength between two components x and y, and a control parameter of the system in our analysis. For $\varepsilon = 0$, x_t and y_t are independent of each other, while for $\varepsilon = 0.5$, x_t and y_t are the same. Here, we used a tent map as a nonlinear function f in each component because the tent map exhibits chaotic dynamics that can result in randomness which is necessary for the random walks we seek here [21]. In addition, the tent map is tractable mathematically (the extension for the other form of the function f or a larger number of components are described in the Supplementary Information). The tent map f we used is the following:

$$f(x) = \begin{cases} \frac{x}{r} & (x < r), \\ \frac{1-x}{1-r} & (x \geq r) \end{cases}$$

where r is a parameter of the deformation of tent maps. In our study, we set $r = 0.7$, but the main conclusion does not qualitatively depend on r (Fig. S4). The general model for such systems includes globally coupled models that are used for modeling a class of nonlinear systems, including neural networks [35].

Finally, we simply define the movement of the agent determined by x_t and y_t, and assume the absolute angle θ_t and the turning angle $\Delta\theta_t$ of the agent at t are as follows:

$$\theta_{t+1} = \theta_t + \Delta\theta_t$$

$$\Delta\theta_t = c(x_t - y_t)$$

where c is a magnitude parameter for regulating the scale of the direction changes. We set c as $\pi/\max(|x_t - y_t|)$ because the maximum difference between x_t and y_t should correspond to the largest turning angle, π or $-\pi$. Practically, c was obtained for each run using $t = 1, ..., 10^4$ in advance. The velocity of the movements of the agents is kept constant, and thus we assume that the velocity is equal to one unit space per time step. Therefore, the position $\boldsymbol{X_t} = (X_t, Y_t)$ of the agent can be updated at each time t:

$$X_{t+1} = X_t + \cos(\theta_t)$$

$$Y_{t+1} = Y_t + \sin(\theta_t).$$

The larger the differences between the two outputs, the larger the turning angles are. In contrast, consecutive small differences (e.g., approx. zero) between the outputs can produce movements of straight lines as $\theta_{t+1} \approx \theta_t$. Note that we do not assume any specific probability distribution, including power law distributions, and thus the process is completely deterministic. Moreover, the parameter and function form of the system is symmetric for x and y because we expect non-biased movements for right and left.

The initial conditions of x and y were drawn from a uniform distribution $(0, 1)$ randomly and independently. Then, we ran and abandoned the first 10^3 steps because there is a possibility that the initial state is not on an attractor. The time after the first 10^3 is denoted by $t = 0$. The initial position $\boldsymbol{X_0} = (X_0, Y_0)$ in the 2-dimensional space was set to be $(0, 0)$. We consider a featureless environmental space with no borders, so the agents obtain no stimuli from the environment. Even in such conditions, they can move around in space (Fig. 1B-D). Therefore, the movement is classified as spontaneous behavior resulting from internal states such as brain dynamics.

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Evaluation of movement trajectory

To evaluate the movement trajectories produced by the agents, we used a rigorous method for fitting probability distributions to the step length distribution, as well as empirical studies [30, 31, 32]. Humphries et al. [32] proposed a robust method for the analysis of movement trajectories, in which the two-dimensional trajectory is mapped onto two one-dimensional axes, X and Y. We analyzed only one of them, because our model is non-biased in terms of the X and Y axes. Then, the step lengths of the consecutive and same directional movements were evaluated based on a maximum likelihood estimation (see the details in [31]). Note that the minimum step length was set to 1 in the analysis because we know that it is 1 in the simulation.

Moreover, to characterize the property of diffusion we calculated the mean squared displacement (MSD) defined as:

$$\mathrm{MSD} = \langle (\boldsymbol{X_t} - \boldsymbol{X_0})^2 \rangle$$

where $\langle \cdot \rangle$ represents the ensemble average for trajectories with different initial states.

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