4th International Conference on
Development and Learning and on Epigenetic Robotics
October 13-16, 2014. Palazzo Ducale, Genoa, Italy

A model for biological motion detection based on motor prediction in the dorsal premotor area

Yuji Kawai, Minoru Asada, and Yukie Nagai
Graduate School of Engineering, Osaka University
2-1 Yamada-oka, Suita, Osaka, 565-0871 Japan
Email: {yuji.kawai, asada, yukie}@ams.eng.osaka-u.ac.jp

***Abstract*—Recent findings regarding dorsal premotor area (PMd) activation during observation of smooth biological movements suggest that this motor-related area detects biological motions. We hypothesize that a neural network in the PMd acquires an invariance of self-induced motor commands for smooth movements and interprets the observed biological motions as ones satisfying the invariance in self-movements. To verify our hypothesis, we developed a recurrent neural network (RNN) to be trained with smooth motor movements, and examined how the RNN acquires biological invariance. The results showed that predictive learning of the RNN contributed to invariance acquisition, which enabled it to detect biological motions. Our findings agree with the fact that the PMd originally functions as a motor predictor. Moreover, this RNN could judge the ankle and wrist trajectories of a walking human as biological regardless of the subject's sex and emotional state.**

I. Introduction

Recent neuroscientific studies have described activity in motor-related brain areas during observation of others' actions. The most typical example is the mirror neuron system, including the ventral premotor area [1], but more recent studies have reported activations in the dorsal premotor area (PMd) during observation of a biological motion [2]–[4]. Casile et al. [3] found stronger activations in the PMd, superior frontal gyrus, and middle frontal gyrus on observation of a biological smooth trajectory than on observation of a non-smooth trajectory. The biological motions used in this experiment are defined by the one-third power law, in which the tangential speed is proportional to the one-third power of the radius of curvature [5]. This law, where speed decreases with a larger curvature, holds for many biological motions (e.g., hand trajectories [5] and eye movements [6]). Thus the law is known as kinematic invariance of biological motions. Observers who watch the movements with the invariance consider them as natural human or biological movements [7]. These studies suggest that the PMd is involved in detection of biological motions, though its mechanism is not well understood.

It is reported that even neonates, who have little visual experience, are able to distinguish between biological and non-biological motions [8]–[10]. Assuming that the ability is not innate, it seems to be acquired through motor experience during the fetal period rather than visual experiences. Indeed, smooth and voluntary reaching actions in the fetal period [11] and one-third power law-like hand movements during the neonatal period have been observed [12]. Thus, it is inferred that neonates acquire the biological invariance of motor commands without visual information and detect biological motion based on the invariance.

The PMd is activated during the planning, execution, imagination, and observation of reaching actions [13], [14]. It is noted that this area strongly reacts to an error between observed and predicted self-limb trajectories based on motor commands [15]. A reaction to the prediction error also occurs during the observation of others' reaching actions [16]. The motor prediction required by the error detection seems to be computed in the PMd. Neurons in this area anticipatorily activate for both the execution of a self-reaching action and observation of another individual's movement [17]. Namely, they represent the motor prediction before the execution and the observation of the movement. Wolfensteller et al. [18] reported activations in the PMd during a prediction task in which a subject predicted the next position of a moving object. This area is also activated when a subject imagines moving their own arm [18].

Based on the existing evidence, we hypothesize that a neural network in the PMd acquires the kinematic invariance of self-induced motor commands and detects biological motions by comparing observed trajectories with those which were predicted based on the invariance. That is, the PMd judges observed trajectories as biological motions if their prediction errors are small enough (i.e., the trajectories exhibit the invariance of self-induced motor commands). We propose a computational model based on this hypothesis and investigate what characteristics of the neural network are required to represent the kinematic invariance, such as the one-third power law, by computer simulations. Specifically, we examine the importance of motor prediction in detecting biological motions, which is a function of the PMd.

The main role of the proposed model is to acquire the invariance of biological motions, such as the one-third power law. It has been reported that trajectory planning of human-like biological motions can be modeled by minimizing the jerk (i.e., the derivative of acceleration) [19], which satisfies the one-third power law [20]. In our first experiment, we examine whether a neural network that learned minimum-jerk trajectories can acquire the invariance shared by the one-third powers law. Here, a problem is that the trajectories according to the one-third power law do not always have minimum jerk. The one-third power law is defined by an

equation that includes a curvature, which thus is a function of acceleration. The neural network, therefore, should generalize its internal representation from minimum-jerk trajectories (a rule of jerk) to those satisfying the one-third power law (a rule of acceleration) over a derivative gap. In the next experiment, we fed the trajectories of point light display (PLD) of human walkers into the neural network and test whether it can identify them as biological motions. A previous study raised the possibility that humans can perceive a biological motion from a trajectory out of PLD of living organisms [21], and the trajectories of walkers' PLD are reported to discriminate between sexes [22] and emotional states [23]. We investigate effects of these properties of walkers on the invariance acquired by the neural network.

A. Related work and our originality

The work by Giese and Poggio [24] is well-known as a computational model of PLD recognition in the visual cortex. This model integrates locally observed motions into global motion information along the visual path from the primary visual area to the superior temporal sulcus, which is then associated with a gait label (e.g., walking or running) by supervised learning. Their model represents a process of global motion information in the higher visual areas. Conversely, we aimed to explain a mechanism of biological motion detection in the motor-related area. We hypothesize that this ability is acquired from self-induced motor commands, which is supported by studies showing that neonates with little visual experience can detect biological motions [8]–[10].

An existing model posits that a recurrent neural network (RNN) extracts invariances of reaching movements by predictive learning, although it does not aim to explain the neural mechanism in humans [25]. This RNN learned the time-series positions of an arm and a hand during reaching behaviors, which acquired representations of angles of the arm and horizontal positions of a hand. However, the position data were limited to a reaching context, so the representations were specific only for reaching movements. In contrast, our model extracts the invariance more generally from smooth biological motions regardless of the types of actions and modalities (vision or motor commands). Furthermore, our model complies with the neuroscientific evidences for motor prediction and error detection in the PMd.

II. A Model for Biological Motion Detection

Fig. 1 depicts an overview of the proposed model. The blue and red boxes correspond to the superior parietal lobule/visual areas and PMd, respectively. Firstly, the model learns to predict time-series velocities of motor commands and acquires the invariance of self-movements, such as smooth kinematic profile (solid arrows in Fig. 1). The model, learned based on self-induced motor commands, is subsequently given a time-series of velocities of observed motions and evaluates whether the motions satisfy the self-kinematical invariance based on prediction errors (broken arrows in Fig. 1). If the errors are small (i.e., if the observed motions have the same invariance

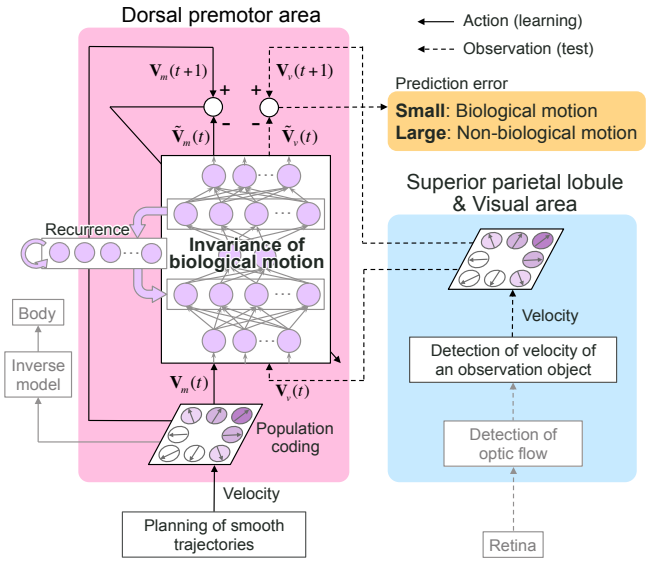


Fig. 1. A model for biological motion detection in the dorsal premotor area. The predictor learns smooth self-motor trajectories and first acquires an invariance of biological motions (arrows of the solid lines). The predictor is then input the velocities of an observed object and regards the motion as a biological one if the prediction error is small (arrows of the broken lines).

as the self-motor commands), the motions are interpreted as biological ones. Else, the model regards them as non-biological motions.

The motor commands generating smooth trajectories to end points are given by the minimum-jerk model [19]. A velocity (a direction $\theta(t)$ [deg], and a magnitude $v(t)$) of a trajectory at a given time t is coded as activations of eight neurons with direction selectivities at intervals of 45 degrees, each of which is calculated by:

$$v_i(t) = v(t) \exp\left(-\frac{(\theta(t) - 45i)^2}{2\sigma^2}\right) \quad (i = 1, \cdots, 8), \qquad (1)$$

where σ is a constant. A vector $\boldsymbol{V}_m(t)$ consists of these neural populations is fed into a predictor, which learns to minimize the error between its output $\tilde{\boldsymbol{V}}_m(t)$ and a subsequent input $\boldsymbol{V}_m(t+1)$. It is expected that this predictive learning allows the model to acquire the invariance of motor commands.

The predictor that acquired the invariance of self-motor commands subsequently evaluates whether or not observed motions are biological. The time-series velocities of an observed object are coded in the same manner as motor commands in an environment-coordinate system ($\boldsymbol{V}_v(t)$), which is an input of the predictor in the observation phase. The predictor compares the output $\tilde{\boldsymbol{V}}_v(t)$ with the next input $\boldsymbol{V}_v(t+1)$. It then judges the observed smooth motions to be biological if the prediction errors are small, that is, if the observed motions possess the invariance acquired from self-induced motor commands.

It is known that velocities of hand movements are coded by neurons with direction selectivities in the PMd [26]. A population coding method similar to ours (Eq. (1)) has been reported

to be able to decode activations of monkeys' neurons in the PMd during their hand movements, resulting in reconstruction of the hand trajectories according to the one-third power law [27]. Neurons in the middle temporal (MT) area represent the velocity of an observed object using population coding [28], suggesting that this is a general coding method for motions irrespective of modality.

The RNN we used as the predictor is a sandglass [29], which is consist of five layers and one context layer type (a central part of the red box in Fig. 1). It is known that a three-layered neural network with many neurons in a middle layer can acquire arbitrary non-linear mappings. Our neural network combines such two three-layered networks in series, which enables non-linear compression of input data [30], [31]. The compact representation acquired in the middle layer avoids over-fitting and helps the network's generalization. We integrate a recurrent structure with the five-layered neural network, which returns information from the fourth layer to the second through the context layer. The connection weights between the fourth and context layers and the self-recursive weights in the context layer are constants, whereas the others are learned by back-propagation.

III. Experiment

A. Experimental setting

1) Input data: Neural network input consists of motor commands of limbs movements given by a minimum-jerk model [19]. We generated five two-dimensional (2D) minimum-jerk trajectories as learning data. The positions, velocities, and accelerations of initial points, via points, and terminal points, as well as the times at via points were determined in a random manner. The movement duration was 2.0 s, and a sampling rate was 20 Hz (every 0.05 s). We made additional 10 minimum-jerk trajectories along different pathways using the learning data as ideal visual (test) data in observing biological movements. The trajectories satisfying the one-third power law are not always minimum jerk. We made 10 trajectories according to the one-third power law to investigate whether the model, which learned from minimum-jerk trajectories, could acquire biological invariance (e.g., the one-third power law). The trajectories generated by the one-third power law had the same paths and elapsed times at terminal points as the minimum-jerk ones but slightly shifted via points. We also generated 10 trajectories as non-biological motions with the same paths and elapsed times at terminal points as the minimum-jerk ones but at constant tangential speeds. The velocities of all trajectories were normalized from 0 to 1, and were then coded as activities of a neural population by Eq.(1).

We used the PLD of 28 walkers (14 men and 14 women; mean age 22.5 years, range 17–28 years) as real biological motions from the database of three-dimensional (3D) PLD of humans walking: Body Movement Library [32]. Each walker has four emotional states: neutral, angry, happy, and sad. The temporal resolution was down-sampled from 60 Hz to 20 Hz. Each point on a body is normalized to fix the waist in a space like a general stimulus for presentation in psychological experiments. We only used four points on the elbow, wrist, knee, and ankle because of their large displacements. They were normalized and coded in the same manner as the artificial trajectories. Fig. 2 shows trajectories of the body parts of a male walker, whose emotional state is natural.

The numbers of neurons in the five layers of the RNN were set to 8, 15, 2, 15, and 8 from the first layer and σ in Eq.(1) was 60 in all experiments. The weights for self-recursive connections in the context layer and the learning coefficient for back-propagation of this RNN were set to 0.8 and 0.01, respectively. The initial weights were given in a random manner between -0.5 and 0.5 and were updated 10,000 times. We evaluated each test pattern based on the squared error averaged over the trajectories.

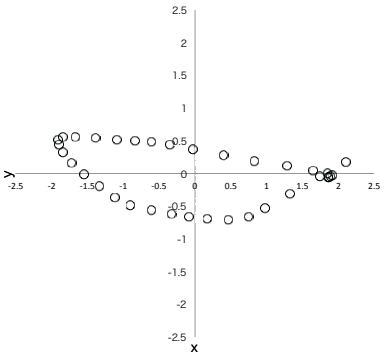
2) Procedure: In Experiment 1, the neural network learned minimum-jerk trajectories; and then unknown trajectories satisfying minimum jerk, the one-third power law, and constant speed were input into the model. It is expected that output errors for the trajectories satisfying minimum jerk and the one-third power law are small, while those with a constant speed are large. We investigated the best conditions to acquire the biological invariance by comparing the output errors between neural networks with two factors: learning tasks and network structures. In the former, a neural network learned to minimize prediction errors (i.e., Error $= \{\tilde{\boldsymbol{V}}(t) - \boldsymbol{V}(t+1)\}^2$) or perform identity mapping (i.e., Error $= \{\tilde{\boldsymbol{V}}(t) - \boldsymbol{V}(t)\}^2$). The latter factor indicates whether or not a neural network has a recurrent structure (i.e., an RNN or a feedforward neural network [FNN]).

We investigated whether the model, which learned from minimum-jerk trajectories, could generalize its internal representation to those adhering to the one-third power law if the input included both velocities and trajectory accelerations in the second experiment, while the input for Experiment 1 included only velocities. It is inferred that the input including the velocities and accelerations allows the model to more easily acquire biological invariance and thus to be more predictable because the one-third power law is a function of an acceleration. However, the input may cause over-fitting to the learning patterns so that the jerk is minimum. The trajectory accelerations were computed by differences of the velocities and were coded by a neural population. The model learned the prediction of the velocities and the accelerations of the minimum-jerk trajectories. We then compared the prediction errors generated by the RNN and FNN.

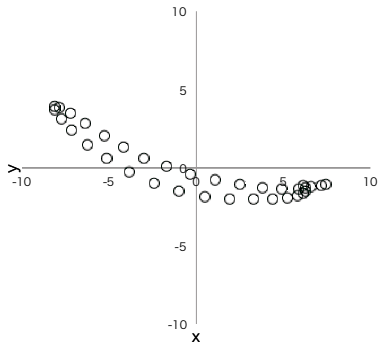
The last experiment examined whether the model could interpret the trajectories of PLD as biological motions. We input the PLD data to the RNN, which learned the time-series prediction of velocities in Experiment 1. The prediction errors were averaged over the walkers for each emotional state and body part.

B. Result

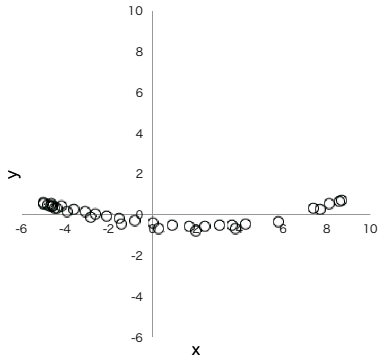
1) Learning task and network structure to acquire biological invariance: The mean error in each network condition is summarized in Table I. One-way ANOVAs (Error $\times$ Test



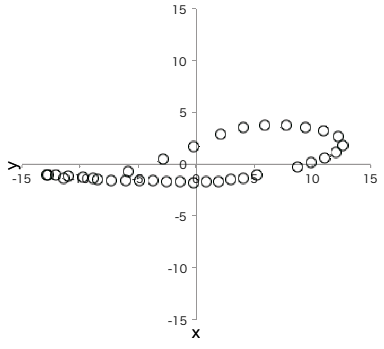
(a) Elbow



(b) Wrist



(c) Knee



(d) Ankle

Fig. 2. Trajectories of body parts while a man is walking with a natural emotional state.

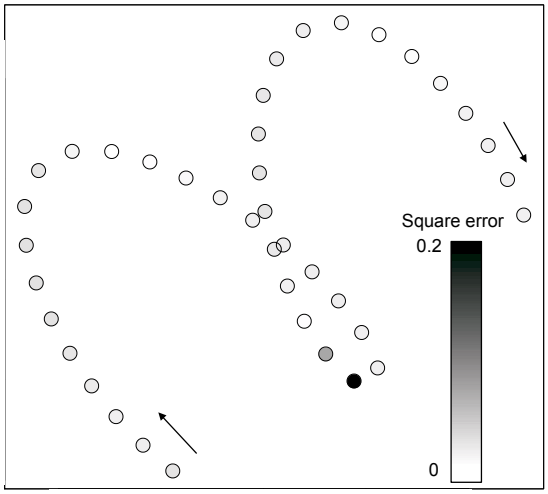


Fig. 3. A square error distribution when an unknown trajectory with a constant speed is input to an RNN learned prediction of the minimum-jerk trajectories. The color depths of points at regular time intervals denotes the magnitudes of the prediction errors.

pattern) revealed that there were significant main effects of test patterns when the RNN learned prediction ($p < .01$) and when the RNN ($p < .05$) or FNN ($p < .01$) learned identity mappings. *Post hoc* testing (Bonferroni) for predictive learning by the RNN revealed that the errors for the minimum-jerk trajectories were not significantly different from the ones for the trajectories by the one-third power law ($p = .90$), and the errors for the trajectories satisfying the minimum jerk or the one-third power law were significantly smaller than the constant speed errors (either ps $< .01$). This RNN therefore generalized its internal representation to trajectories with the one-third power law and can distinguish between biological-like trajectories and those with constant speed. In contrast, the FNN could not evaluate biological motions based on the output errors, even if it learned to predict the motions. Although the neural network that learned identity mappings resulted in significant effects of the test patterns, the errors for the minimum-jerk trajectories were the largest. This was due to the difference of the maximums of test patterns: the maximums of input of the minimum jerk, the one-third power law, and the constant speed trajectories were 0.81, 0.54, and 0.48, respectively. The models only acquired the identity mappings, so the errors were more sensitive to the input magnitude than trajectory smoothness.

Fig. 3 depicts the prediction error distribution of an RNN that learned prediction along a trajectory with constant speed. A sampling rate is constant, and the gray coloring indicates the magnitude of the square error at the time point shown. This figure demonstrates that the errors were larger at the points with large curvatures. Thus, errors at large curvatures enable the model to detect biological motions more easily.

2) Learning of time-series velocity and acceleration: Table II shows the prediction errors estimated by the RNN or FNN,

TABLE I
MEAN SQUARED ERRORS WHEN THE TEST PATTERS WERE INPUT INTO THE MODEL THAT LEARNED BY THE MINIMUM-JERK TRAJECTORIES.

Task	Structure	Test patterns: Minimum jerk	One-third power law	Constant speed	p
Prediction	Recurrent	0.0053	0.0088	0.020	**
Prediction	Feedforward	0.011	0.012	0.014	n.s.
Identity mapping	Recurrent	0.00074	0.00054	0.00053	*
Identity mapping	Feedforward	0.00075	0.00050	0.00047	**

p denotes results of one-way analyses of variance (ANOVAs) (Error $\times$ Test pattern). n.s.: $p > .05$, *: $p < .05$, **: $p < .01$

TABLE II
MEAN SQUARED ERRORS WHEN THE INPUT WAS A VELOCITY AND AN ACCELERATION

Task	Structure	Test patterns: Minimum jerk	One-third powers law	Constant speed	p
Prediction	Recurrent	0.0022	0.012	0.024	**
Prediction	Feedforward	0.0019	0.011	0.021	**

p denotes results of one-way ANOVAs (Error $\times$ Test pattern). n.s.: $p > .05$, *: $p < .05$, **: $p < .01$

which learned from the velocities and accelerations of the minimum-jerk trajectories. The overall errors were lower than those in Experiment 1, and there was little difference between the RNN and FNN. One-way ANOVAs revealed significant main effects of test patterns under the conditions of both structures (either ps $< .001$). *Post hoc* testing (Bonferroni) revealed significant differences between the minimum-jerk trajectories and the trajectories by the one-third power law, as well as between the trajectories by the one-third power law and those with constant speed regardless of the network structure (both ps $< .01$). Acceleration as input therefore enabled the model to predict the minimum-jerk trajectories more accurately even if the network did not have a recurrent structure. However, these networks over-fitted to the minimum-jerk trajectories and did not generalize its internal representations to the ones satisfying the one-third power law.

3) Human walker trajectories : Fig. 4 shows the prediction errors for four body trajectories averaged over the individuals that were produced by the RNN, which learned prediction of the minimum-jerk trajectories in Experiment 1. The bar colors represent the walkers' emotional states: white, red, yellow, and blue denote neutral, angry, happy, and sad during walking, respectively. The stars on the top of the bars show the significant differences with the mean prediction error for artificial trajectories according to the one-third power law shown in Experiment 1 (solid line). The broken line denotes the mean prediction error for the trajectories with constant speed. All averaged errors for the trajectories of a wrist and ankle were significantly lower than those with constant speed (all ps $< .01$), and some of them did not significantly differ from the ones satisfying the one-third power law. Therefore, the model was able to identify them as biological motions similar to the one-third power law trajectories. Our model did not evaluate the trajectories of the elbow and knee as biological motions because these trajectories changed their velocity during straight-line motions (see Fig. 2 (a) and (b)). A 4 (emotional state: neutral, angry, happy, sad) $\times$ 4 (body part: elbow, wrist, knee, ankle) $\times$ 2 (sex: male, female) $\times$ 28

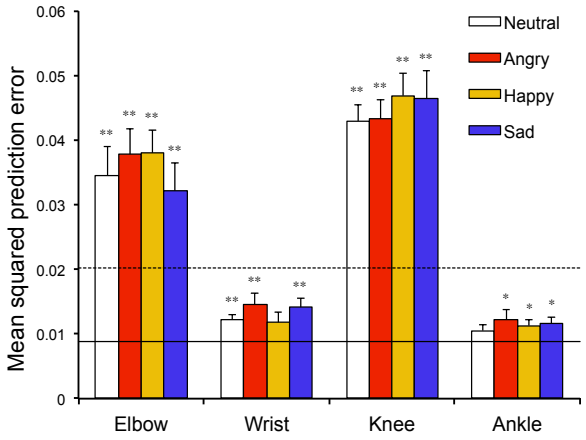


Fig. 4. Mean squared prediction errors for the trajectories of four body parts (elbow, wrist, knee, and ankle) produced by the RNN, which learned to predict the minimum-jerk trajectories in Experiment 1. The bar colors represent the emotional states of the walkers (neutral, angry, happy, and sad). The solid and broken lines show the mean errors for trajectories by the one-third power law and the constant speed, respectively. Stars indicate a significant difference with the solid line (*: $p < .05$, **: $p < .01$). Error bars denote the standard error of the mean.

(individual) mixed ANOVA revealed significant main effects of body part ($p < .01$) and individual ($p < .05$). Therefore, the model that learned from the minimum-jerk trajectories could recognize wrist and ankle trajectories as biological motions, regardless of their emotional states and the sex, whereas it may detect individual differences.

IV. DISCUSSION

We proposed a model that judges whether an observed motion is biological by estimating a prediction error based on an invariance extracted from smooth self-motor commands. A neural network given a series of velocities of minimum-jerk trajectories learned their short-term prediction. The results of Experiment 1 demonstrate that our model could predict unknown minimum-jerk trajectories even if there was a gap

of a second-order derivative between an input variable (velocity) and a characteristic of the learned trajectory (jerk). Furthermore, the model generalized to trajectories by the one-third power law, suggesting that it acquired the biological invariance, including the minimum jerk and the one-third power law. Experiment 1 also revealed that this invariance was only acquired when a neural network with recurrent connections learned to predict trajectories. In order to generalize the internal representation beyond a derivative gap, the model must deal with time-series data for a certain period, as well as with data in the present. In contrast, it does not need for learning of identity mapping to treat data in the past, which prevented the model from acquiring the invariance represented by acceleration and jerk. Thus, the acquisition of the invariance was required to store information by a recurrent structure and utilize the past information by predictive learning.

Many neuroimaging studies have shown that the prediction of an observed motion is one of functions of the PMd [18], [33], [34]. The PMd also reportedly copes with the execution and imagination of self-limb movements, as well as the observation of others' movements [14], [16], [18], suggesting that this motor-related area seems to predict an observed motion based on a self-motor representation. The importance of prediction indicated by our simulation is consistent with these neuroimaging findings, which supports the validity of our model. Our simulation showed that the recurrent structure was required to acquire the invariance. Other model studies of the premotor area (e.g., [35], [36]) also suggested the necessity of a recurrent structure. Collectively, the evidence suggests that the learning and control of time-series movements might require neural processing with a recurrent structure.

The model input was assumed to be velocities due to the neurophysiological facts [26], [28]. The acquisition of the invariance of the one-third power law (i.e., a function of acceleration) is needed to process a time-series data by recurrent connections. Nevertheless, Experiment 2 showed that input including a velocity and an acceleration enabled the network to learn the invariance even if it does not have a recurrent structure. The network, however, over-fitted to the minimum jerk (i.e., a characteristic of small acceleration changes), causing a sudden decline in the model's generalization capacity. In order to acquire the biological invariance by predictive learning of minimum-jerk trajectories, a velocity is sufficient for an input variable, and it is important to generate a representation of an acceleration in an RNN. To our knowledge, the neuron populations that represent the accelerations of motor commands in the PMd have not been described. This may be a reason for that neurons in this region improve the generalization capacity for a predictive function.

The common biological invariance of motor commands and visual information allowed the model to evaluate biological motions. We solved the differences between the modalities (coordination systems) by the population coding of local motion information that is common between them. Previous neuroscience studies have reported that the velocities of motor commands [26] and an observed object [28] are represented in population coding. This plausible coding method enables the model to input motor and visual data to a common predictor, resulting in an extraction of the invariance, independent of the modalities.

The results of Experiment 3 indicated that the model could judge the actual wrist and ankle trajectories of human walkers as biological motions regardless of the subjects' sex or emotional state. One psychological study reported that humans can recognize the trajectories of walkers' body parts as biological [37]. Troje [38] suggested a hierarchical model for the perception of biological motions that is comprised of higher layers for pattern recognition of actions, sex, and emotional states from global motion information and a lower layer for biological motion detection from a local trajectory. Our simulation results showing that the detection of biological motions was insensitive to the walkers' sex and emotional states suggest that our model corresponds to the lower-level processing described in Troje's model [38]. However, our model was able to detect individual differences because it was sensitive to trajectory jerk and the dataset including some jumping-like gaits. It is expected that a psychological study will investigate the relationship between the individual gait differences and the perception of biological motions.

One of the most interesting phenomenon is that neonates who have had minimal visual experience can discriminate biological motions and trajectories by the one-third power law from non-biological motions [8]–[10]. Although previous studies concluded that the ability to detect biological motions is innate, our model suggests the possibility that it is acquired through fetal and neonate motor experience. However, previous studies also reported that neonates prefer upright biological motions to inverted ones [8], [9], which cannot be explained by our model because of a lack of gravity perception. It is known that neonates have a nearly mature vestibular system, which senses gravity [39]. Motor commands generate smooth trajectories that are optimized in an environment with gravity, which may enable the model to replicate the inversion effect in biological motion perception. Furthermore, it is reported that atypical kinematics profiles (e.g., greater jerk) of arm movements of subjects with autism correlate with their low sensitivity of minimum-jerk trajectories [40]. Our model may provide a theoretical explanation for these developmental phenomena. Further studies clarifying how self-motor function affects social recognition (e.g., biological motion detection) from a developmental perspective are desirable.

V. Conclusion

We hypothesized that the PMd predicts the velocity of an observed object based on the invariance of self-motor commands of smooth limb movements and evaluates whether or not the observed motion is biological based on the prediction error. We devised a model to detect biological motion that satisfies the neuroscientific constraints that the PMd represents velocities of motor commands and predicts one's own and others' movements. Our simulations revealed that predictive learning realized by a neural network with a recurrent structure

is needed to acquire biological invariance, such as the one-third power law from minimum-jerk trajectories, which agrees with the facts in neuroscience. Predictive learning enables the model to learn and generalize its internal representation beyond a derivative gap between the input (velocity) and variables comprising desired invariance (acceleration and jerk). The model successfully discriminated wrist and ankle trajectories of walking humans from non-biological motions, irrespective of the walkers' sex and emotional states.

ACKNOWLEDGMENT

The authors gratefully acknowledge advices by Dr. Chisato Yoshida in Kyoto University. This work was supported by JSPS Grants-in-Aid for Specially Promoted Research (24000012) and Grants-in-Aid for JSPS Fellows (13J00756).

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