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J Neurophysiol 94:395-399, 2005. First published Feb 16, 2005; doi:10.1152/jn.01168.2004

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Testing Bayesian Models of Human Coincidence Timing

Makoto Miyazaki,¹ Daichi Nozaki,² and Yasochi Nakajima¹

¹Department of Rehabilitation for Sensory Functions and ²Department of Rehabilitation for Movement Functions, Research Institute of National Rehabilitation Center for Persons with Disabilities, Tokorozawa, Saitama, Japan

Submitted 11 November 2004; accepted in final form 13 February 2005

Miyazaki, Makoto, Daichi Nozaki, and Yasochi Nakajima. Testing Bayesian models of human coincidence timing. *J Neurophysiol* 94: 395–399, 2005. First published March 2, 2005; doi:10.1152/jn.01168.2004. A sensorimotor control task often requires an accurate estimation of the timing of the arrival of an external target (e.g., when hitting a pitched ball). Conventional studies of human timing processes have ignored the stochastic features of target timing: e.g., the speed of the pitched ball is not generally constant, but is variable. Interestingly, based on Bayesian theory, it has been recently shown that the human sensorimotor system achieves the optimal estimation by integrating sensory information with prior knowledge of the probabilistic structure of the target variation. In this study, we tested whether Bayesian integration is also implemented while performing a coincidence-timing type of sensorimotor task by manipulating the trial-by-trial variability (i.e., the prior distribution) of the target timing. As a result, within several hundred trials of learning, subjects were able to generate systematic timing behavior according to the width of the prior distribution, as predicted by the optimal Bayesian model. Considering the previous studies showing that the human sensorimotor system uses Bayesian integration in spacing and force-grading tasks, our result indicates that Bayesian integration is fundamental to all aspects of human sensorimotor control. Moreover, it was noteworthy that the subjects could adjust their behavior both when the prior distribution was switched from wide to narrow and vice versa, although the adjustment was slower in the former case. Based on a comparison with observations in a previous study, we discuss the flexibility and adaptability of Bayesian sensorimotor learning.

INTRODUCTION

Our sensorimotor system often requires that motor responses are timed precisely in accordance with the behavior of a certain external target. For example, to hit a pitched ball while playing baseball or cricket, the batter has to control the timing of the swing based on the speed of the ball. Such timing behavior, which is referred to as coincidence timing, has been studied extensively in sports science (e.g., Ripoll and Latiri 1997; Williams et al. 2002). Because the external environment that we usually encounter is variable, not constant, we need to monitor visual and other sensory signals to estimate the current behavior of the external target accurately. Naturally, these sensory signals are exposed to internal and external noise (Körding and Wolpert 2004; van Beers et al. 2002), so they cannot always provide sufficient information for precise estimates. To compensate for the sensory uncertainty, prior knowledge or experience of the target behavior is helpful information for the estimation. By observing the external target behavior

for a long time, we can determine its predictable probabilistic structure. Considering various phenomena in our world, such as human behavior and physical events, the trial-by-trial variability has a certain probabilistic structure, such as a Gaussian distribution (e.g., Chen et al. 1997). That is, the speeds of all pitched balls do not appear with the same probability; their frequency distribution should have a peak(s) at a certain speed(s) and higher and lower speeds should occur less frequently. Using prior knowledge of such a probabilistic structure, we should be able to realize a more rational estimation of the current target's behavior.

In conventional studies of timing, the probabilistic structure of the external targets that we encounter in our daily life has been largely ignored, although many studies have focused on the properties of the variability in the processing system, i.e., the brain (e.g., Ding et al. 2002; Gibbon et al. 1997; Vorberg and Wing 1996; Wing and Kristofferson 1973). The Bayesian framework (Bayes 1763; Bernardo and Smith 1994) tells us that our CNS can estimate objects or events in the environment optimally by integrating the current sensory input and prior knowledge of the probabilistic structure of these objects or events. Phenomena that are consistent with Bayesian integration have been shown in studies of visual perception (Guo et al. 2004; Kersten et al. 1997; Liu et al. 1995; Rao 1999; Weiss et al. 2002). Recently, it was reported that Bayesian integration is used for optimal estimation in the control of sensorimotor tasks, such as spatial reaching (Körding and Wolpert 2004) and force-amplitude matching (Körding et al. 2004). In this study, we tested whether Bayesian integration is also implemented in the coincidence-timing type of sensorimotor control by manipulating the width of the prior distribution of target timing.

METHODS

Subjects

Twelve right-handed subjects (10 males and 2 females; age range, 25–35 yr) participated in this study after giving their informed consent. This study was approved by the ethics committee of the National Rehabilitation Center for Persons with Disabilities.

Apparatus

The stimulus was presented visually using three red LEDs (S1, S2, and S3) that were placed in a horizontal array (Fig. 1A). Each LED was 5 mm in diameter, and the centers of the neighboring LEDs were 20 mm apart. The stimulus set was placed 1.25 m in front of the seated subjects. The LEDs were connected to a pulse generator (AMPI Master-8-vp) that was controlled by a personal computer. The LEDs

Present address for reprint request and other correspondence: M. Miyazaki, Advanced Research Center for Human Sciences, Waseda University, 2-579-15 Mikajima, Tokorozawa, Saitama 359-1192, Japan (E-mail: miyazaki@aoni.waseda.jp, miyazaki_mkt@yahoo.co.jp).

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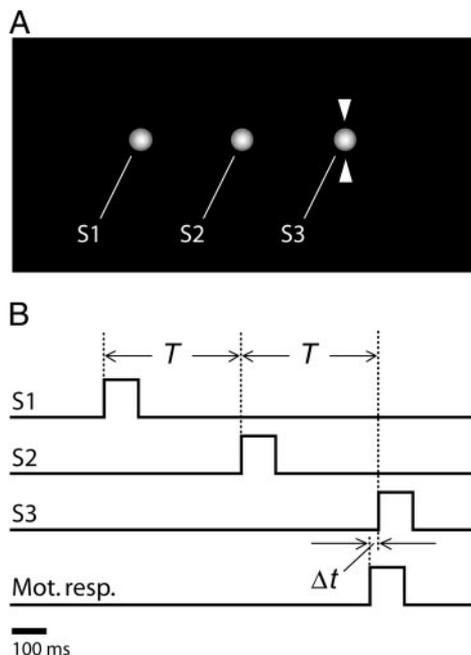


FIG. 1. A: stimuli used in experiment. B: example traces of stimuli and subjects' motor response. Positive Δt values imply premature responses relative to S3 onset, and negative values imply delayed responses.

were lit one after the other in the order S1→S2→S3 (Fig. 1B). The duration of illumination of each LED was 100 ms. In each trial, the temporal interval between S1 and S2 was identical to that between S2 and S3. The time interval between the neighboring LEDs (T) was drawn randomly from a prior Gaussian distribution $p(T_{\text{true}})$ with a mean of 400 ms, and the SD (σ_{prior}) depended on the experimental conditions. The SD was 20 ms for the "narrow distribution" condition and 40 ms for the "wide distribution" condition.

The subjects performed their motor responses by pressing a handheld button using their right thumb. The button had to be depressed 2 mm to switch it on. The button was sprung, and the minimum passive weight required to switch it on was 200g.

Task and procedure

The subjects were required to press the button such that its onset coincided with the onset of S3 based on the perceived information on interval S1-S2 in each trial.

All of the subjects performed 480 trials of this task for each of the two conditions (narrow/wide distribution, see *Apparatus*); consequently, 960 trials were performed in all. Six subjects first experienced the narrow distribution (narrow→wide group), and the remaining six first experienced the wide distribution (wide→narrow group). The intertrial interval was 2.5 s. To maintain a high level of alertness, the subjects were given a 1-min rest between every 80 trials. The subjects were allowed a 20-min rest when changing from one distribution condition to the next.

Data acquisition

The stimuli and switch responses were recorded simultaneously using a data acquisition system (Biopac Systems MP-150); they were digitized at 1,000 Hz and stored on a hard disk during the experiment. Using these records, the timing deviation of the switch onset from the S3 onset (Δt) was measured for each trial (Fig. 1B). Positive Δt values imply premature responses relative to the S3 onset, and negative values imply delayed responses.

Computational models and predictions

Based on the Bayesian framework, the target time interval that the subjects estimated ($T_{\text{estimated}}$) in the current trial can be computed using two parameters: the target time interval that the subjects sensed (T_{sensed}) and the prior distribution of the target time interval $p(T_{\text{true}})$. Depending on the manner in which the subjects used the prior distribution $p(T_{\text{true}})$, the following three different estimation models can be considered (see Körding et al. 2004). To test which model best accounts for the actual human timing estimation, we used the systematic (average) timing deviation ($\langle \Delta t \rangle$) of the subjects. $\langle \Delta t \rangle$ is the systematic deviation of $T_{\text{estimated}}$ from the true target timing, T_{true} , i.e., $\langle \Delta t \rangle \approx \langle T_{\text{true}} - T_{\text{estimated}} \rangle$, where any possible timing bias of the motor responses accounted for by another mechanism (Haggard et al. 2002) is ignored for the sake of approximation. Each of the three models predicts a different behavior of $\langle \Delta t \rangle$ versus T_{true} .

Model 1: Naive estimation

In this model, to obtain $T_{\text{estimated}}$, the subjects ignore $p(T_{\text{true}})$ and depend fully on T_{sensed} . Assuming that there is no bias in the sensory perception, Δt should be zero on average for any T_{true} . Therefore if the subjects use this model, the plots of $\langle \Delta t \rangle$ versus T_{true} should be flat under both the narrow and wide distribution conditions.

Model 2: Optimal Bayesian estimation

In this model, $T_{\text{estimated}}$ is obtained by integrating T_{sensed} and $p(T_{\text{true}})$. The optimal Bayesian estimation can be formulated as follows

$$T_{\text{estimated}} = \frac{\sigma_{\text{sensed}}^2}{\sigma_{\text{prior}}^2 + \sigma_{\text{sensed}}^2} [400 \text{ ms}] + \frac{\sigma_{\text{prior}}^2}{\sigma_{\text{prior}}^2 + \sigma_{\text{sensed}}^2} T_{\text{sensed}}$$

where the SD of σ_{sensed} represents innate noise (variability) in the subject's sensors. Therefore $T_{\text{estimated}}$ can be calculated as a weighted sum of the mean of $p(T_{\text{true}})$ (= 400 ms) and T_{sensed} . This equation implies that when the uncertainty (SD) of the prior distribution decreases, the estimation of the time interval depends more on the mean of the prior; conversely, when the uncertainty of the prior distribution increases, the estimation depends more on the sensed time interval in each trial. Theoretically, this estimation should always result in a smaller mean squared error in comparison with the naive estimation (Körding and Wolpert 2004). Therefore this model can optimize its estimation depending on the widths of the prior distribution, i.e., it is the optimal strategy in dynamic environments that have diverse statistics.

Assuming that there is no bias in the sensory perception, on average, T_{sensed} can be approximated by T_{true} . Therefore this model predicts that $\langle \Delta t \rangle$ ($\approx \langle T_{\text{true}} - T_{\text{estimated}} \rangle$) is linearly dependent on T_{true} , and the slope decreases as σ_{prior} increases, i.e., if the subjects use the optimal Bayesian estimation, the regression line relating $\langle \Delta t \rangle$ to T_{true} should have a greater slope in the narrow distribution condition and a smaller slope in the wide distribution condition.

Model 3: Bayesian estimation with one fixed prior distribution

In this model, although the subjects can use the prior distribution, there is only one fixed prior distribution that is innately defined or cannot be modulated once acquired. It predicts that the plot of $\langle \Delta t \rangle$ against T_{true} should form a sloping line, but its slope should be constant for all values of σ_{prior} , i.e., if subjects use this strategy, the regression line relating $\langle \Delta t \rangle$ to T_{true} should have the same slope in both the narrow and wide distribution conditions. Moreover, note that this model involves an extreme case that is mentioned below. Takahashi et al. (2001) reported that, when subjects experienced a randomly varying force field, they learned the mean of the forces. It has been

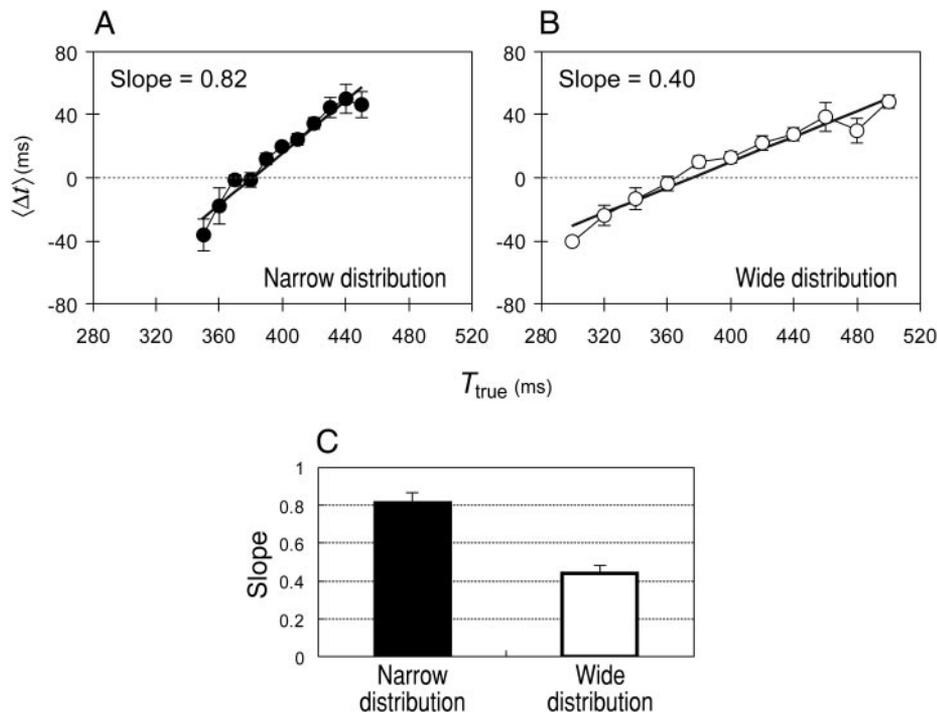


FIG. 2. *A* and *B*: plots of systematic (average) timing deviation $\langle \Delta t \rangle$ vs. true time interval T_{true} for a typical subject (*A*: narrow distribution condition; *B*: wide distribution condition) constructed from the 2nd half of trials for each condition. The subject first experienced the narrow distribution condition. *C*: across-subject values of the slope calculated from the 2nd half of trials for narrow and wide distribution conditions. Error bars in all figures denote SE.

suggested that subjects cannot learn the distribution of forces in a similar random environment (Scheidt et al. 2001). In case the subjects in our experiment learn and use only the mean of the prior, the slope of the regression line should always be unity (slope = 1), regardless of the width of the prior distribution.

RESULTS

Figure 2, *A* and *B*, shows the systematic timing deviation $\langle \Delta t \rangle$ as a function of the true time interval, T_{true} , for a typical subject (*A*: narrow distribution; *B*: wide distribution). These plots were constructed from the second half of the trials (i.e., the last 240 trials) for each condition. The plots of $\langle \Delta t \rangle$ against T_{true} are linear under both conditions, and the regression slope under the narrow distribution condition (0.82) is greater than that under the wide distribution condition (0.40).

To give an overview of the difference in the slopes between the narrow and wide distribution conditions for all subjects, we show the across-subject values for the slope calculated from the second half of the trials for each condition in Fig. 2*C*. The slope is 0.82 ± 0.05 (SE) for the narrow distribution condition and 0.44 ± 0.04 for the wide distribution condition. Zero is far outside the 99.9% confidence interval for both values, i.e., both slopes are significantly >0 , rejecting the prediction of model 1. Subsequently, the slope for the narrow distribution condition is significantly greater than that for the wide distribution condition ($P < 0.001$, paired *t*-test), which differs from the prediction of model 3 but is in accord with that of model 2. Therefore we concluded that the systematic timing behavior of the subjects was coincident with the prediction of the optimal Bayesian model.

In addition, we assessed the uncertainty of the sensory noise, σ_{sensed} , using the measured slopes (see Körding et al. 2004). σ_{sensed} was 42.03 ± 2.72 ms for the narrow distribution condition and 35.49 ± 4.70 ms for the wide distribution condition; the difference was not significant ($P = 0.12$).

There was a positive shift in the relation $\langle \Delta t \rangle$ versus T_{true} along the vertical axis (see Fig. 2, *A* and *B*). The across-subject values of the shift were 21.66 ± 7.83 and 16.21 ± 6.73 ms for the narrow and wide distribution conditions, respectively, indicating that the subjects' motor responses were apt to occur earlier than S3. The Bayesian model does not predict this. Such a premature motor response relative to actual target onset is often observed in human sensorimotor synchronization (e.g., Aschersleben and Prinz 1995; Chen et al. 1997), which can be accounted for by the fact that self-generated movements are perceived as occurring later than they actually do (Haggard et al. 2002).

To detail the time-course involved in learning the prior distribution, we show the slopes as a function of the trial bin for the narrow \rightarrow wide and wide \rightarrow narrow groups (Fig. 3), where the bin size used to calculate the slope was 240 trials, and the window used to examine a bin was shifted by incre-

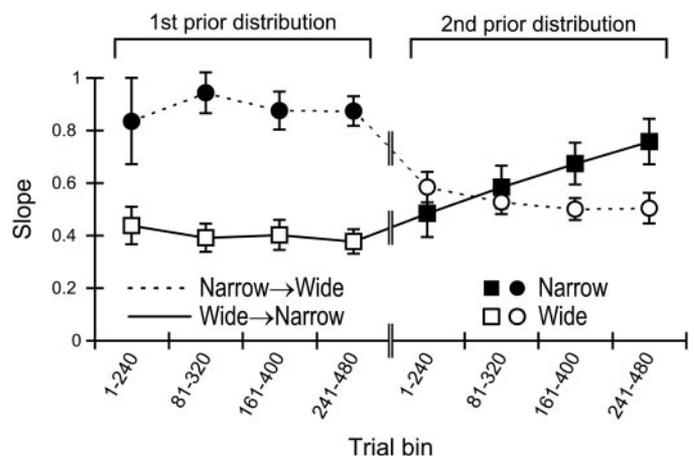


FIG. 3. Across-subject values of the slope of $\langle \Delta t \rangle$ vs. T_{true} as a function of the trial bin for narrow \rightarrow wide (dotted line) and wide \rightarrow narrow (solid line) groups.

ments of 80 trials in each distribution condition. A three-factor ANOVA with two repeated measures revealed that the main effect of group and the interactions of group \times distribution condition and group \times distribution condition \times trial bin were significant ($P < 0.01$). Comparing the slopes across groups, for the first prior distribution, the difference between the narrow and wide prior distributions did not reach significance at the earliest stage, i.e., for the 1–240 trial bin ($P = 0.063$, t -test). The differences were significant for the 81–320, 161–400, and 241–480 trial bins ($P < 0.001$). This indicates that the subjects could attain the appropriate systematic timing behavior for the optimal Bayesian integration by 320 trials at the latest. For the second prior distribution, the difference between narrow and wide distributions was significant only for the 241–480 trial bin ($P < 0.05$). Attending to the within-group change of the slope, for the narrow \rightarrow wide group, two-way repeated-measure ANOVA revealed that the main effect of the distribution condition was significant ($P < 0.05$), whereas the main effect of the trial bin and the interaction of the distribution condition \times trial bin were not significant ($P > 0.4$). A posthoc test (Tukey's HSD) revealed that the decrease of the slope in the second prior distribution was significant for all trial bins as compared with that for the 241–480 trial bin in the first prior distribution. For the wide \rightarrow narrow group, a two-way repeated-measure ANOVA revealed that, whereas the main effect of the distribution condition was not significant ($P = 0.09$), the main effects for the trial bin and the interaction of the distribution condition \times trial bin were significant ($P < 0.05$). The posthoc test revealed that, compared with the 241–480 trial bin in the first prior distribution, the increase in the slope in the second prior distribution was significant for the 81–320, 161–400, and 240–481 trial bins ($P < 0.05$), but it was not significant in the first stage, i.e., for the 1–240 trial bin ($P = 0.48$). These results indicate that the subjects could modulate their systematic timing behavior according to the change in the width of the prior distribution from wide to narrow and from narrow to wide. In addition, more trials are needed for the modulation to reach significance in the wide \rightarrow narrow group as compared with the narrow \rightarrow wide group.

DISCUSSION

Apposite model in human coincidence timing

In this study, we tested whether Bayesian integration is implemented in human coincidence timing by manipulating the width of the prior distribution for the target timing. The systematic timing behavior of the subjects agreed with the prediction of the optimal Bayesian model (model 2). Although a large number of studies based on psychophysical measures have reported the property or mechanism of various biological timing processes (e.g., Delignières et al. 2004; Dunlap 1910; Gibbon et al. 1984; Lee 1976; Spencer et al. 2003; Tresilian 1995; Yamamoto and Kitazawa 2001), to the best of our knowledge, our report is the first to show that the optimal Bayesian model can be applied to such a domain. Our finding that the human sensorimotor system should use Bayesian integration while performing a *timing* task, as well as spacing (Körding and Wolpert 2004) and force-grading (Körding et al. 2004) tasks, supports the argument that Bayesian integration might be fundamental to all aspects of human sensorimotor control and learning (Körding and Wolpert 2004).

Adaptability to the novel prior distribution: differences from a study of force grading

A similar manipulation of the prior distribution was used in a study of force-amplitude matching (Körding et al. 2004). In that task, $\geq 1,000$ learning trials were needed before the significant difference predicted by the optimal (full) Bayesian model was found in the systematic force-grading behavior between two groups that encountered narrow and wide prior distributions. In contrast, in our timing task, the systematic timing behavior of the two groups differed within several hundred trials of learning. Furthermore, in force grading, the subjects who experienced the narrow prior distribution condition first were able to adjust their systematic force-grading behavior according to the subsequent wider distribution, whereas the subjects who experienced the wide prior distribution condition first could not significantly adjust their behavior according to the subsequent narrower distribution. In contrast, in our experiment, the subjects were able to adjust their behavior significantly, as predicted by the optimal Bayesian model, not only when the prior distribution was switched from narrow to wide but also when it was switched from wide to narrow. The differences between the two results suggest that the human sensorimotor system has greater flexibility in acquiring and updating prior knowledge for time estimation than in the case of force estimation.

Guo et al. (2004) argued that the prior knowledge used for the Bayesian estimation in visual perception could be classified into built-in and experience-based types. The former depends on the invariant statistics in the natural environment and is probably permanently embedded in relatively lower cortical areas, such as V1. The latter depends on the recent experience of the observer and might involve higher cortical areas. This argument attributes the presence of plasticity of prior knowledge to where it is represented in the brain. Brain imaging and neurophysiological studies indicate that different brain areas engage in the execution of time- and force-relevant tasks, whereas some areas in close proximity work on both tasks in common. Rao et al. (2001) showed that the basal ganglia, bilateral premotor cortex, right inferior parietal cortex, and right dorsolateral prefrontal cortex are associated with the processes involved in time-interval discrimination. Meck and Benson (2002) emphasized the role of the frontal-striatal circuit in interval timing. In addition, the cerebellum is considered to play a crucial role in timing (Ivry and Spencer 2004). In a precision-grip task, relevant activation was observed in the right ventral premotor area, rostral cingulate motor area, and several locations in the posterior parietal and prefrontal areas (Ehrsson et al. 2000). Perhaps the difference in behavioral flexibility to a change in the prior distribution is accounted for by the difference in the brain areas that engage in acquiring or storing the prior information for either timing or force grading, although we cannot yet nominate the area(s) involved.

Adaptability to the novel prior distribution: a common property with a study of force grading

Although the subjects were able to adjust their behavior significantly, as predicted by the optimal Bayesian model, even when the prior distribution was switched from wide to narrow in our timing task, a difference was observed in the speed of

the adjustment. More trials were needed for the adjustment to reach significance when the prior distribution was switched from wide to narrow than vice versa. Note that the difference in the adjustment speed agreed with the above-mentioned result for force-amplitude matching. If the number of trials for the second prior distribution had been increased in the experiment by Körding et al., the adjustment of behavior might have reached significance even when the prior distribution was switched from wide to narrow. Therefore the observations for both force-grading and timing tasks indicate that, whereas the human sensorimotor system is swift to adapt to a narrow-to-wide change in the prior distribution, it is slow to adapt to a wide-to-narrow change. If further studies confirm that such a difference in adaptation speed is a universal property of Bayesian integration in sensorimotor learning, this will provide a clue to how prior distribution is acquired and maintained in the human CNS.

ACKNOWLEDGMENTS

We thank Dr S. Kitazawa for helpful comments on this paper.

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