

Research Letter

Is Subcellular Localization Informative for Modeling Protein-Protein Interaction Signal?

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Statistical methods have been intensively applied in genomic signal processing (Dougherty et al. 2005). For budding yeast *Saccharomyces cerevisiae* with around 6000 proteins, genome-wide protein-protein-interaction (PPI) (Fromont-Racine et al. 2000, Ito et al. 2001, Newman et al. 2000, and Uetz et al. 2000 among others) and protein subcellular localization (PSL) (Huh et al. 2003) data recently became available and for the latter the presence of 4152 proteins is experimentally tested in each of the 22 subcellular compartments. Recent work shows that multiple biological sources are helpful for both PSL and PPI predictions, and this paper studies statistical feasibility of modeling PPI from PSL since PSLs may play different marginal or joint roles in the complex regulatory network. However, our results indicate that PSL may be controversial for this purpose as an independent source.

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1. STATISTICAL METHODS

1.1. Two-way PPI count contingency table

We extracted 2712 PPIs from MIPS [1] which were available at <http://hto-b.usc.edu/~msms/AssessInteraction/MIPSMATCHYPD.txt> as of 2005 and used by Lin and Zhao [2] for PPI network robustness study. We use 1641 PPIs with complete PSL information in Huh et al. [3], for example, protein A has a 22-dimensional PSL vector $\tilde{L}_A = (L_{A,1}, L_{A,2}, \dots, L_{A,22})$, where $L_{A,i} = 1$ represents presence of protein A at PSL i and $L_{A,i} = 0$ represents absence of protein A at PSL i . For proteins A and B, we create 44-dimensional PSL vector $\tilde{L}_{AB} (\tilde{L}_A, \tilde{L}_B)$ along with an exchanged counterpart $\tilde{L}_{BA} (\tilde{L}_B, \tilde{L}_A)$ for naive balance. Since log-linear model with large number (2^{44}) of cross-classified cells may lack power where the total PPI count is relatively small ($<10,000$), we instead explore an alternative two-way (22^2) contingency table whose rows (compartments: $i = 1, \dots, 22$) and columns

(compartments: $j = 1, \dots, 22$) jointly assign each PPI into cell (i, j) with one protein in compartment i and the other one in compartment j ($i, j = 1, 2, \dots, 22$) (Figure 1). Note that one PPI may be redundantly counted due to multiple PSL occupation. Cytoplasm and nucleus likely play crucial roles since these two compartments hold most PPI entries and other compartment pairs have much less entries. Negative binomial model avoids overdispersion and shows ER to Golgi, lipid particle and nucleus may be significant effects for this two-way contingency table.

1.2. PSL correlation pattern

For 44-dimensional joined PSL vectors we calculate all $C_{44}^2 + C_{44}^1 (= 990)$ pairwise Pearson correlation coefficients

$$\text{Corr}(\tilde{L}_{AB}, \tilde{L}_{AB}) = \begin{bmatrix} \text{Corr}(\tilde{L}_A, \tilde{L}_A), \text{Corr}(\tilde{L}_A, \tilde{L}_B) \\ \text{Corr}(\tilde{L}_B, \tilde{L}_A), \text{Corr}(\tilde{L}_B, \tilde{L}_B) \end{bmatrix}. \quad (1)$$

This calculation was carried over to the following four disjoint sets of protein pairs: (1) interacting protein pairs from PPIs (set [1]), (2) non-PPI protein pairs from those proteins with PPI (set [2]), (3) non-PPI protein pairs from those proteins without PPI (set [3]), and (4) non-PPI protein pairs from combining protein without PPI and protein with PPI (set [4]). As in Section 1.1, by selecting those PPIs (MIPS) with PSL information (Huh et al. [3]), we obtained 2883 proteins without PPI, 3282 exchanging PSL vectors for (set [1]), 1 591 338 exchanging PSL vectors for (set [2]), 8 308 806 exchanging PSL vectors for (set [3]) and 7 317 054 exchanging PSL vectors for (set [4]). 30% of non-PPI protein pairs and 69% of PPI protein pairs have colocalization, thus 31% of PPIs may be transient. The pseudoimages and contour plots for PSL correlations (1) are given in Figure 2, where the upper-left quadrat in panel 1 shows significant between-protein colocalization pattern for (set [1]) and no clear colocalization pattern occurs for between-protein PSLs for (sets [2,3,4]). These observations motivate us to study if between-protein PSL pattern could potentially discriminate between protein pairs with PPI and those without PPI.

1.3. Retrospective logistic regression

We propose a realistic model for quantifying PPI tendency from fused PSLs of proteins A and B (with exchanging). The PSL and PPI information is expressed as

$$\begin{aligned} (L_{A,1}, L_{A,2}, \dots, L_{A,22}, L_{B,1}, L_{B,2}, \dots, L_{B,22}) &\sim I_{AB}, \\ (L_{B,1}, L_{B,2}, \dots, L_{B,22}, L_{A,1}, L_{A,2}, \dots, L_{A,22}) &\sim I_{BA}, \end{aligned} \quad (2)$$

where $I_{AB} (= I_{BA})$ is the binary PPI indicator (response) and the logistic regression model is proposed to be logit

$$\begin{aligned} \Pr(\text{PPI} | A, B) = \beta_0 &+ \sum_{i=1}^{22} \beta_i (L_{A,i} + L_{B,i}) \\ &+ \sum_{i < j} \beta_{ij} (L_{A,i} L_{A,j} + L_{B,i} L_{B,j}) \\ &+ \sum_{i \leq j} \beta'_{ij} (L_{A,i} L_{B,j} + L_{B,i} L_{A,j}), \end{aligned} \quad (3)$$

where β_0 and β_i imply default PPI probability and PPI tendency of single protein with PSL i , β_{ij} , and β'_{ij} represent PPI tendency of single protein with PSLs i and j and two proteins with PSLs i and j , respectively, where $i = j$ describes PPI tendency of two proteins with common PSL i . The number of model parameters is $1 + 2C_{22}^1 + 2C_{22}^2 = 507$. For efficiency we consider a reduced model $\beta_0 + \sum_{i \leq j} \beta'_{ij} (L_{A,i} L_{B,j} + L_{B,i} L_{A,j})$ which incorporates second-order PSL effects between two proteins. The yeast interactome and proteome are inherent libraries and not subject to arbitrary experimental design, which indicates a retrospective (case-control) study. On the other hand, we have $\sim 18 \times 10^6$ total protein pairs and only $\sim 2 \times 10^3$ PPIs in our data. In order to overcome computer memory limitation and achieve reasonable sample sizes for both case (PPI) and control (non-PPI) groups, we need to select out a sample subset under statistical justification. For logistic model with responses y_i s and predictors x_i s, we let

Z_i indicate whether subject i is selected and assume $\rho_1 = \Pr(Z_i = 1 | y_i = 1)$ and $\rho_0 = \Pr(Z_i = 1 | y_i = 0)$, both of them are free of x_i . If the logistic model based on all subjects has $\text{logit}(\Pr(y_i = 1 | x_i)) = \alpha + \beta x_i$, then the retrospective logistic regression (RLR) after selection probability adjustment would be $\text{logit}(\Pr(y_i = 1 | x_i, z_i = 1)) = \alpha + \log(\rho_1/\rho_0) + \beta x_i$ (Chapter 4.3.3, McCullagh and Nelder [4]). We apply case selection probability 1 and control selection probability 2×10^{-3} (3282 PPIs, 38 338 entries and 254 parameters) and identify around 60 significant effects. The resultant prospective PPI probabilities are to be adjusted based on foregoing theory.

1.4. PPI prediction from PSL

After fitting the preceding model, we apply certain threshold τ to the simple classification rule

$$\begin{aligned} \Pr(\text{PPI} | \tilde{L}_{AB} \text{ or } \tilde{L}_{BA}) > \tau &\implies \text{PPI}, \\ \Pr(\text{PPI} | \tilde{L}_{AB} \text{ or } \tilde{L}_{BA}) \leq \tau &\implies \text{non-PPI}. \end{aligned} \quad (4)$$

We randomly divide the whole dataset for retrospective study into 10 disjoint portions. Each portion (includes PPIs and non-PPIs in proportion) acts as one testing set and the other nine portions are combined into one training set for 10-fold cross validation. We classify each protein-protein pair in the testing set into PPI or non-PPI by comparing the calculated probabilities (from trained model parameters) with some threshold τ . We find that PPI probability median of the non-PPI subset in the training set is always equal to that of the PPI subset in the training set and the PPI probability median (1.88×10^{-4}) for PPI subset also equals that of non-PPI subset for the whole dataset in retrospective study. For retrospective study with PPI probability median threshold, we have specificity around 98% and sensitivity around 15%, RandomForest Breiman [5] in R reaches specificity around 99% and sensitivity around 20% and support vector machine (SVM) in R reaches specificity around 50% and sensitivity around 90%. The PPI probabilities from retrospective study dataset and 10-fold cross-validation are plotted in Figure 3. The logistic model-based classification results are found to be sensitive to threshold. If we use “ $\Pr(\text{PPI} | \tilde{L}_{AB} \text{ or } \tilde{L}_{BA}) \geq \tau \implies \text{PPI}$ ” and “ $\Pr(\text{PPI} | \tilde{L}_{AB} \text{ or } \tilde{L}_{BA}) < \tau \implies \text{non-PPI}$ ”, where τ equals PPI probability median, then we obtained very different classification results. After prospective PPI probability adjustment, the threshold-based classification (4) is applied to the complete PPI and PSL data ([Sets 1,2,3,4], Section 1.2) and the resultant ROC curve is given in Figure 4 with area under curve (AUC) less than 0.5. Since we may simply invert this classifier to make AUC greater than 0.5, Figure 4 indicates that the proposed logistic regression model ((3) in Section 1.3) may not be highly sufficient even if this model is carefully chosen. We also observe the following facts: selection procedure in retrospective study may involve some bias, the joined PSL patterns (from two proteins) are finite with uncertain overlap between PPI set and non-PPI set, false positives and false negatives may exist in both PPI and PSL data and others. From statistical point of view, interprotein PSL pattern may not independently determine PPI tendency,

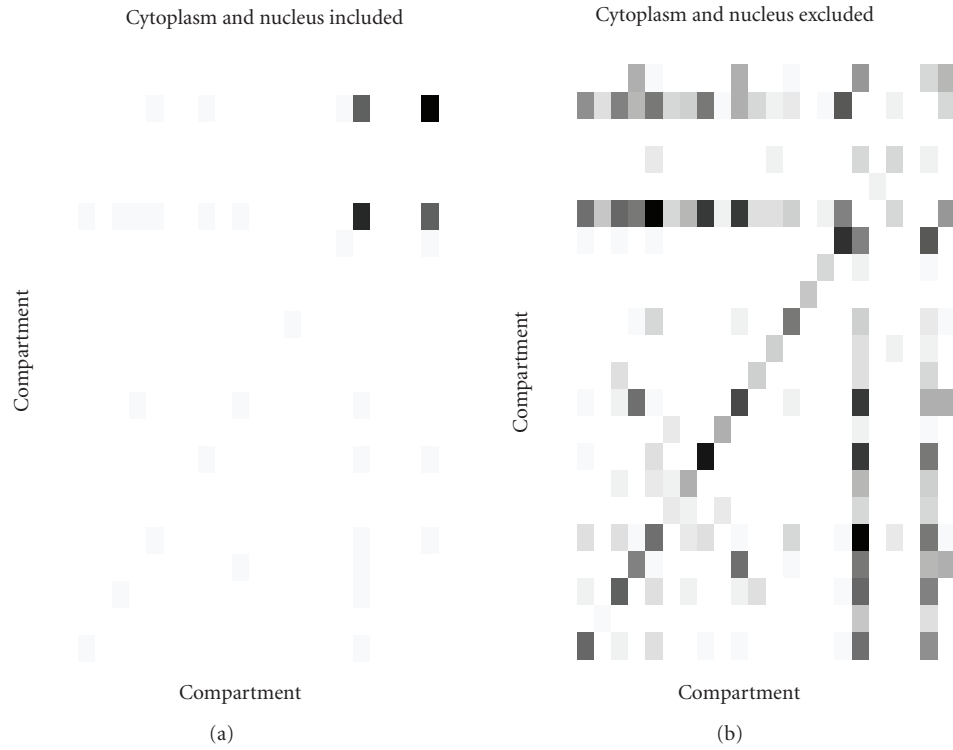


FIGURE 1: Pseudoimages for two-way PPI count contingency table by combining pairwise PSLs (Section 1.1). The left panel includes cytoplasm and nucleus and the right panel excludes cytoplasm and nucleus. From left (bottom) to right (top) on the $x(y)$ -axis: compartments [1 : 22].

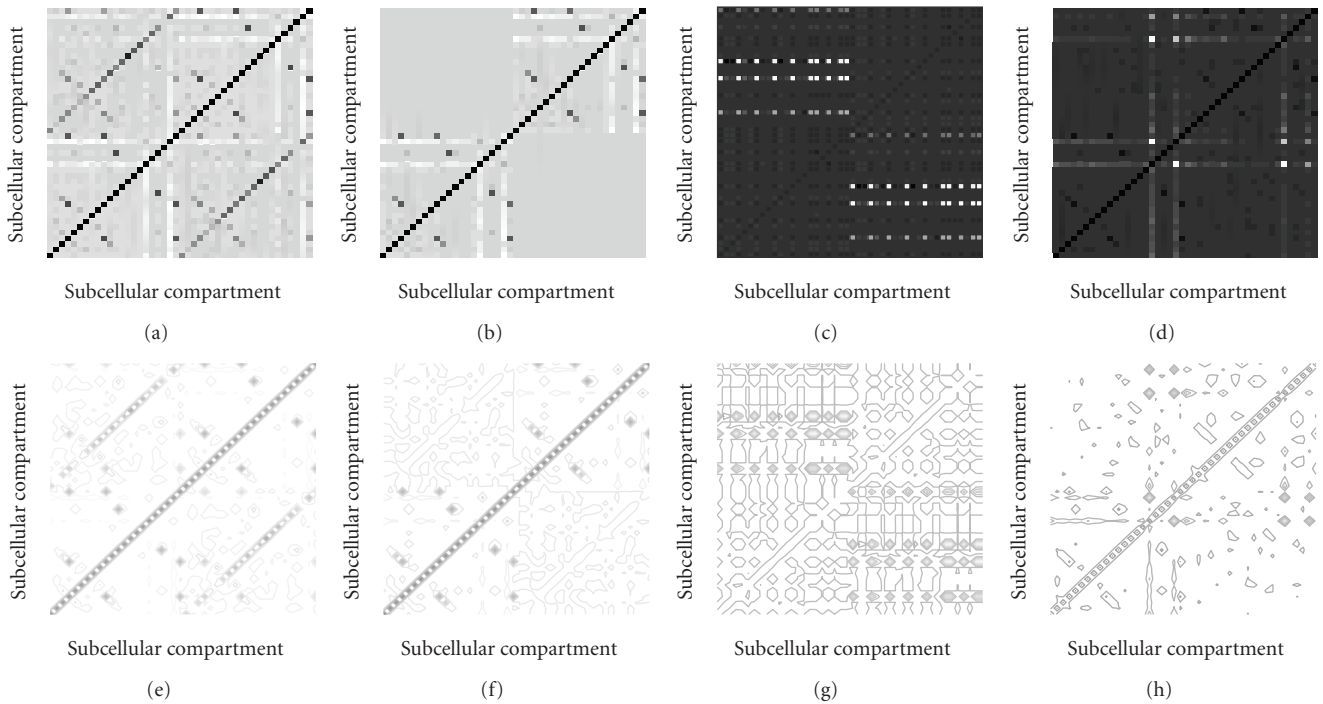


FIGURE 2: Correlation pseudoimages and contour plots for PPIs (set [1]: panel 1) and non-PPIs (sets [2,3,4], panels 2, 3, 4). From left (bottom) to right (top) on the $x(y)$ -axis in each panel: compartments [1 : 22] for protein $A(B)$.

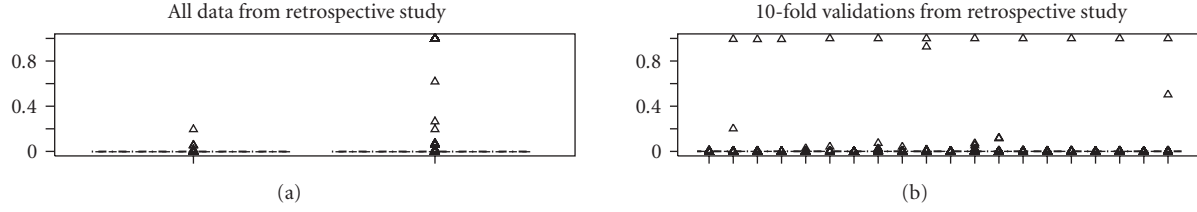


FIGURE 3: (Top panel) PPI probabilities from retrospective study. (Lower panel) PPI probabilities from 10-fold cross-validation (after prospective adjustment), each pair of consecutive boxplots is for individual testing set where PPI subset follows non-PPI subset.

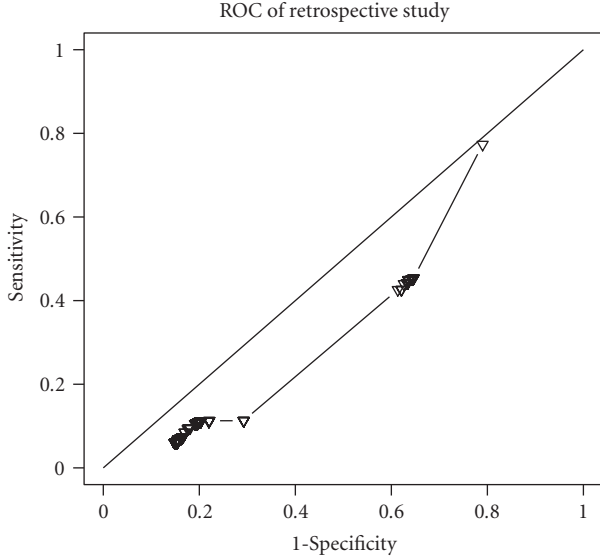


FIGURE 4: ROC (∇ connection) based on prospective PPI probability (adjusted from retrospective study) threshold-based classification.

and threshold-based PPI prediction rule may not discriminate PPI from non-PPI either. The former conclusion is also a major concern from biologists who consider PPI mechanism far beyond only PSL information.

2. DISCUSSION

In this article, we proposed statistical analysis of the association between PPI and PSL with the possibility of offering clues for further specific biological experiments. The aforementioned model is only one possible approach out of many helpful tries. It is likely that a totally different approach based on PSL information may lead to disparate results. As an alternative, if we could describe the distribution of 44-dimensional joined binary PSL vectors given PPI or non-PPI: $\Pr(\tilde{L}_{AB} | \text{PPI})$ and $\Pr(\tilde{L}_{AB} | \text{non-PPI})$, then armed with some prior PPI probability, say $\Pr(\text{PPI}) = 3 : (1.8 \times 10^4)$, we can predict PPI probability for joined PSL pattern \tilde{L}_{AB} by Bayes rule

$$\Pr(\text{PPI} | \tilde{L}_{AB}) = \frac{\Pr(\tilde{L}_{AB} | \text{PPI}) \Pr(\text{PPI})}{Q}, \quad (5)$$

where $Q = \Pr(\tilde{L}_{AB} | \text{PPI}) \Pr(\text{PPI}) + \Pr(\tilde{L}_{AB} | \text{non-PPI}) \Pr(\text{non-PPI})$. Section 1.2 is essentially an attempt to work on either the PPI or non-PPI set to study PSL pattern without considering the non-PPI or PPI counterpart, which may be only a matter of exploring $\Pr(\tilde{L}_{AB} | \text{PPI})$ or $\Pr(\tilde{L}_{AB} | \text{non-PPI})$ separately. However, the explicit probability of high-dimensional binary vector is difficult to be constructed. Empirical approaches (Sections 1.1 and 1.2, Huh et al. [3]) offer informative results from different perspectives. On the other hand, Liu et al. [6] modeled PPI based on domain-domain interaction information and computational PSL prediction from other sources which are also feasible, the readers are referred to Lu et al. [7], Szafron et al. [8], Höglund et al. [9], Horton et al. [10], Guda [11], Yu et al. [12], and Zhang et al. [13, 14] among many others.

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Special Issue on Interference Management in Wireless Communication Systems: Theory and Applications

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Interference is a fundamental nature of wireless communication systems, in which multiple transmissions often take place simultaneously over a common communication medium. In recent years, there has been a rapidly growing interest in developing reliable and spectral efficient wireless communication systems. One primary challenge in such a development is how to deal with the interference, which may substantially limit the reliability and the throughput of a wireless communication system. In most existing wireless communication systems, interference is dealt with by coordinating users to orthogonalize their transmissions in time or frequency, or by increasing transmission power and treating each other's interference as noise. Over the past twenty years, a number of sophisticated receiver designs, for example, multiuser detection, have been proposed for interference suppression under various settings. Recently, the paradigm has shifted to focus on how to intelligently exploit the knowledge and/or the structure of interference to achieve improved reliability and throughput of wireless communication systems.

This special issue aims to bring together state-of-the-art research contributions and practical implementations that effectively manage interference in wireless communication systems. Original contributions in all areas related to interference management for wireless communication systems are solicited for this special issue. We are particularly interested in manuscripts that report the latest development on interference channels or cognitive radio channels from the perspectives of information theory, signal processing, and coding theory. Topics of interest include, but are not limited to:

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Special Issue on Network Coding for Wireless Networks

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The main idea in network coding was introduced in 2000 by Ahlswede et al. With network coding, an intermediate node in a network cannot only forward its incoming packets but also encode them. It has been shown that the use of network coding can enhance the performance of wired networks significantly. Recent work indicates that network coding can also offer significant benefits for wireless networks.

Communications over wireless channels are error-prone and unpredictable due to fading, mobility, and intermittent connectivity. Moreover, in wireless networks, transmissions are broadcast and can be overheard by neighbors, which is treated in current systems as interference. Finally, security poses new challenges in wireless networks, where both passive and active attacks have quite different premises than in wired networks. Ideas in network coding promise to help toward all these issues, allowing to gracefully add redundancy to combat errors, take advantage of the broadcast nature of the wireless medium and achieve opportunistic diversity, exploit interference rather than be limited by it, and provide secure network communication against adversarial attacks.

In this special issue, we are interested in original research articles which can carry the momentum further and take the wireless network coding research to the next level. The areas of interest include novel network code designs and algorithms, new applications of wireless network coding, network coding capacity, and performance analysis. In addition to original research articles, we are open to review articles. The following list indicates topics of interest which is by no means exhaustive:

- Network codes and algorithms for wireless networks
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