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Entrainment range affected by the difference in sensitivity to light-information between two groups of SCN neurons*

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The mammals can not only entrain to the natural 24-h light–dark cycle, but also to the artificial cycle with non 24-h period through the main clock named suprachiasmatic nucleus in the brain. The range of the periods of the artificial cycles which the suprachiasmatic nucleus (SCN) can entrain, is called entrainment range reflecting the flexibility of the SCN. The SCN can be divided into two groups of neurons functionally, based on the different sensitivities to the light information. In the present study, we examined whether the entrainment range is affected by this difference in the sensitivity by a Poincaré model. We found that the relationship of the entrainment range to the difference depends on the coupling between two groups. When the coupling strength is much smaller than the light intensity, the relationship is parabolic-like, and the maximum of the entrainment range is obtained with no difference of the sensitivity. When the coupling strength is much larger than the light intensity, the relationship is monotonically changed, and the maximum of the entrainment range is obtained when the difference is the largest. Our finding may provide an explanation for the exitance of the difference in the sensitivity to light-information as well as shed light on how to increase the flexibility of the SCN represented by widening the entrainment range.

Keywords: SCN network, circadian rhythm, coupling strength, sensitivity to light-information, entrainment range

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1. Introduction

Behavioral and physiological rhythms in the living beings are regulated by the main clock, suprachiasmatic nucleus (SCN) of the brain.[1–5] One main function of the SCN is to entrain the body rhythms to the environmental light-darkness cycle. The SCN can entrain to not only the natural 24-h light–darkness cycle but also to the artificial non 24-h light–darkness cycles. For example, a Sudanian grass rat can entrain from 22.9 h (lower limit entrainment) to 25.3 h (higher limit entrainment), a southern flying squirrel can entrain from 23.5 h to 24.9 h, and a human being can entrain from 21.5 h to 28.6 h.[6–9] The range between the lower limit entrainment (LLE) and upper limit entrainment (ULE) is called entrainment range, which reflects the flexibility of the SCN, *i.e.*, the larger the entrainment range is, the larger the flexibility is. The entrainment range is often represented by the LLE in the mathematical model, provided that the LLE and the ULE are symmetrical to 24 h.[6]

The entrainment range is one kind of collective behaviors of about 2.0×10^4 SCN neurons.[5,6] The SCN neurons can be divided into two distinct groups, *i.e.*, the ventrolateral part (VL) and the dorsomedial part (DM), based on the different functions. The VL containing around 25% SCN neurons, and the DM composed of the rest 75% SCN neurons, differ in the sensitivity to the photic information.[9–14] Most of the VL neurons can directly receive the photic information from the retina, while most of the DM neurons can not. The DM neurons receive the information from the VL neurons. Additionally, the coupling is directed between VL and DM due to the neurotransmitters and the directed synapses. The neurotransmitters differ between the VL and the DM.[15–17] The VL neurons produce the vasoactive intestinal polypeptide (VIP) which is absorbed by both the VL and the DM neurons, and the DM neurons are coupled through the arganine vasopressin (AVP). The VL neurons dominate the DM neurons also because the synapses mostly project from the VL. Therefore, the coupling strength from the VL to the DM is larger than the other directions.[5]

This difference in the sensitivity to the photic information plays a key role in the function of the SCN, such as recovery from the jet-lag. In particular, in the beginning days after the jet-lag, the VL switches to the new environmental time immediately because the VL neurons are directly sensitive to the light information, while the DM remains the previous time information. Due to the directed coupling, the DM is gradually synchronized to the VL and reaches the new environmental time in the following days.[13,18] Another experiment is that exposed to a 22-h light–dark cycle, the dissociation between the VL and the DM emerges.[8,11] Two periodic components

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of behavioral activities are observed, *i.e.*, one component of 22-h period, which is equal to the period of the external cycle, is controlled by the VL, and the other component of about 24-h period, which is close to the endogenous period of the SCN, is regulated by the DM.

Recently, by contrary, it has been found that the light-responsive neurons are not located in the specific subregion of the SCN.[19,20] Not only the VIP neurons receive the light information from the retina but also the AVP neurons do. Therefore, both the VL and the DM neurons are sensitive to the light information, directly. Interestingly, the study implied that the VIP neurons can be activated at low light levels whereas AVP neurons require higher light intensities. Accordingly, the sensitive strength to light information differs between the VL neurons and the DM neurons, *i.e.*, the strength is larger in the VL neurons than the DM neurons.

In all previous modeling studies as best as we know, all the SCN neurons were assumed to be sensitive to the photic information with the same strength,[16,21–23] or only the VL neurons are light-sensitive but the DM neurons are light-insensitive.[9,24] Thus far, it is unknown about the effects of the difference in the sensitivity to the light-information. In the present study, we will examine the effects of this difference on the entrainment range based on a Poincaré model. The rest of this article is organized as follows. In Section 2, a Poincaré model is introduced to mimic the SCN. The numerical results and the theoretical explanations are presented in Section 3. At last, we show the conclusions and discussions in Section 4.

2. Description of the Poincaré model

In the present study, the Poincaré model composed of N neuronal oscillators is introduced to mimic the SCN network exposed to an artificial external light–dark cycle.[24–32] For each neuronal oscillator, there are two variables, *i.e.*, x and y. The oscillators are coupled through the mean field F to form an all-to-all network. The model is described as follows:

$$\begin{aligned}
\dot{x}_i &= \gamma x_i(a-r_i) - \frac{2y_i\pi}{\mu_i\tau} + g_iGF + l_iL\sin(\Omega t),\\
\dot{y}_i &= \gamma y_i(a-r_i) + \frac{2x_i\pi}{\mu_i\tau}, \quad i = 1,2,\ldots,N,\\
F &= \frac{1}{N}\sum_{i=1}^{N} x_i,
\end{aligned} \tag{1}$$

where the parameters γ, a, $\mu_i\tau$, and Ω are the relaxation parameter, the intrinsic amplitude, intrinsic periods of the individual oscillators, and environmental frequency, respectively. In order to simulate the nonidentity of the neuronal periods, μ_i satisfies a normal distribution of the mean being equal to 1 and the standard deviation β. The parameter r_i is the amplitude of the i-th oscillator which reads

$$r_i = \sqrt{x_i^2 + y_i^2}, \quad i = 1,2,\ldots,N. \tag{2}$$

The coupling term and the light-input term are g_iGF and $l_iL\sin(\Omega t)$, respectively, where G and L are coupling strength and light intensity, respectively. The key parameters g_i and l_i depend on the region of the neurons, which represents the sensitivity to the mean field and the sensitivity to the light information for oscillator i, respectively. For simplicity, the SCN neurons are divided into two groups to represent the VL and the DM. We assume that for the neurons within the same group, the values of g_i or l_i are the same. If the neuron i is located in the first group of the SCN, *i.e.*, $0 < i \le N_1$, we let $g_i = p$ and $l_i = q$, and if the neuron j is located in the second group of the SCN, *i.e.*, $N_1 < j \le N$, $g_j = (N - N_1 p)/(N - N_1)$, and $l_j = (N - N_1 q)/(N - N_1)$, where the parameters p and q satisfy $(1/N)\sum_i^N g_i = 1$ and $(1/N)\sum_i^N l_i = 1$. Specially, when the numbers of neurons are the same ($N_1 = N - N_1$) for these two groups, the parameters are simplified as $g_j = 2 - p$ and $l_j = 2 - q$ ($N_1 < j \le N$).

The key parameter q represents the difference in the sensitivity to the photic information between the two groups. If $q = 1$, there is no difference. If $q > 1$ (or $q < 1$), the sensitivity of the first group is larger than the second group (or *vice versa*). Similarly, p represents the direction of the coupling between the two groups. If $p = 1$, the coupling is undirected. If $p > 1$ (or $p < 1$), the VL dominates the DM (or *vice versa*). In the results, we will examine whether the difference represented by q affects entrainment range (represented by the LLE). For the numerical simulation, the parameters are set as $a = 1$, $\gamma = 1$, and $\tau = 24$. Without special statement, the number is $N = 2$, *i.e.*, one oscillator represents the VL and the other is DM, and the deviation is $\beta = 0$.

3. Numerical results

Figure 1 shows illustrative examples for the effects of the sensitivity q on the entrainment of the SCN exposed to the light–dark cycle of 22-h period with selected values of parameters. In panel (a), when the value is $q = 0.75$, both the VL and the DM are not entrained to the external cycle, because the phase difference between each group and the external cycle fluctuates over time. In panel (b), when the value increases to $q = 1.25$, both the VL and the DM are entrained to the external cycle, because the phase difference is stable over time. In panel (c), when the value is $q = 1.75$, both the VL and the DM are not entrained to the external cycle, again. Therefore, the value of q influences the entrainment of the SCN to external cycle.

In this section, we will examine the relationship of LLE to the sensitivity q with given values of G and L in Figs 2–4. Because it is unknown that whether the focused neuron is influenced by the coupling term more or the light term more, we select the coupling strength $G = 0.05$, 0.1, and 0.15, respec-

tively, and the light intensity $L = 0.05$, 0.1, and 0.15, respectively.

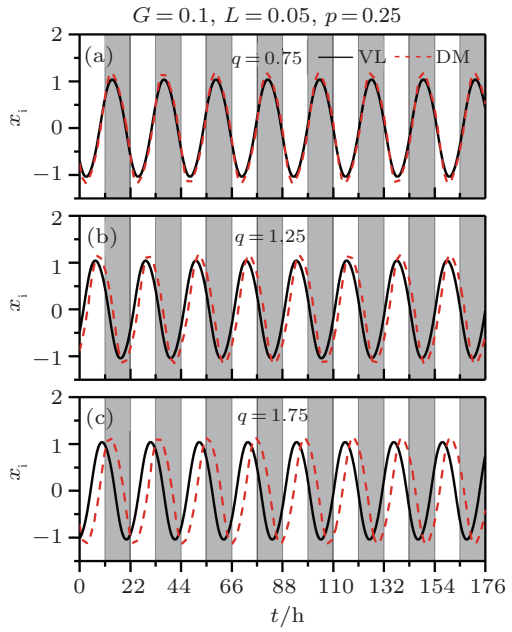


Fig. 1. Illustrative examples for the effects of q on the entrainment of the SCN exposed to the light–dark cycle of 22-h period. The value of q is $q = 0.75$ in panel (a), $q = 1.25$ in panel (b), and $q = 1.75$ in panel (c). The parameters are set as $G = 0.1$, $L = 0.05$, and $p = 0.25$. The grey region and the white region represent the night time and day time, respectively.

The parameters are set as $G = 0.1$, and $L = 0.05$, 0.1, and 0.15 in Fig 2. In panel (a) with $L = 0.05$ ($L < G$), the relationship is monotonously decreasing or increasing in the cases of $p \neq 1$. In particular, when $p = 0.0$ or $p = 0.5$, the relationship is negative; when $p = 1.5$ or $p = 2$, the relationship is positive; and when $p = 1.0$, the LLE is a constant of around 21.9 h. In panel (b) or panel (c), with $L = 0.1$ or 0.15 ($L \geq G$), the relationship is altered to be parabolic-like, in each case of p. If q is smaller than the trough q_c, the LLE decreases with the increase of q, and if q is larger than the trough q_c, the LLE increases with the increase of q for each case of p in panel (b) or panel (c). It is visible that the values of q_c depend on the value of p in each panel of Figs. 2(a)–2(c). Consequently, the quantitative relationship of q_c to p with distinct values of L is plotted in panel (d). In the case of $L = 0.05$, q_c is far away from 1, *i.e.*, q_c is around 2 if $p < 1$, and q_c is around 0 if $p > 1$; in the case of $L = 0.1$, q_c decreases with the increase of p which is from 1.4 to 0.6; in the case of $L = 0.15$, q_c is around 1.25 if $p < 0.8$, and q_c is around 0.75 if $p > 1.2$. Therefore, the function of q_c on p depends on the values of L. With the larger value of L, the function is closer to the line $q_c = 1$.

Next, we also examine the cases of $G < 0.1$ and $G > 0.15$, respectively. The parameters are set as $G = 0.05$ in Fig. 3 and $G = 0.15$ in Fig. 4. The following results are compared with Fig. 2. With $L = 0.05$, the relationship of the LLE to q is similar in Fig. 4(a), whereas the parabolic relationship of LLE to q emerges for each case of p in Fig. 3(a). With $L = 0.1$ or $L = 0.15$, there are also parabolic relationships, however, the values of trough are altered. In Figs. 3(b) and 3(c), the trough q_c is closer to 1 for each case of p, and in Figs. 4(b) and 4(c), the trough q_c is further from 1 for each case of p. Figures 3(d) and 4(d) confirm the dependence of q_c on both p and L.

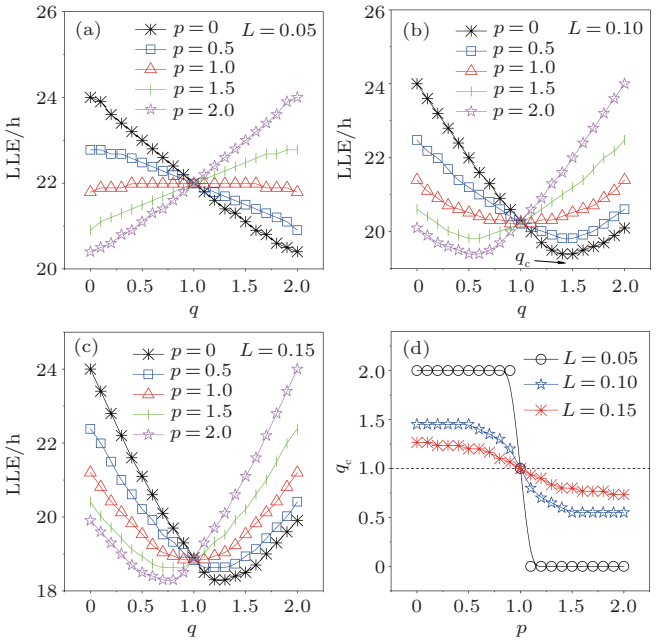


Fig. 2. The effect of the sensitivity q on the lower limit entrainment (LLE) with $G = 0.1$. The parameter L is 0.05, 0.1, and 0.15 in panels (a)–(c), respectively. The relationship of the LLE to q is monotonous for cases of $p \neq 1$ in panel (a), and is parabolic-like for each case of p in panel (b) or panel (c). In panel (d), the relationship of the trough q_c to p is shown. As an example, the trough in the case of $p = 0$ is indicated by q_c in panel (b). Note that larger LLE corresponds to smaller entrainment range. The dashed line indicates the line of $q_c = 1$ in panel (d).

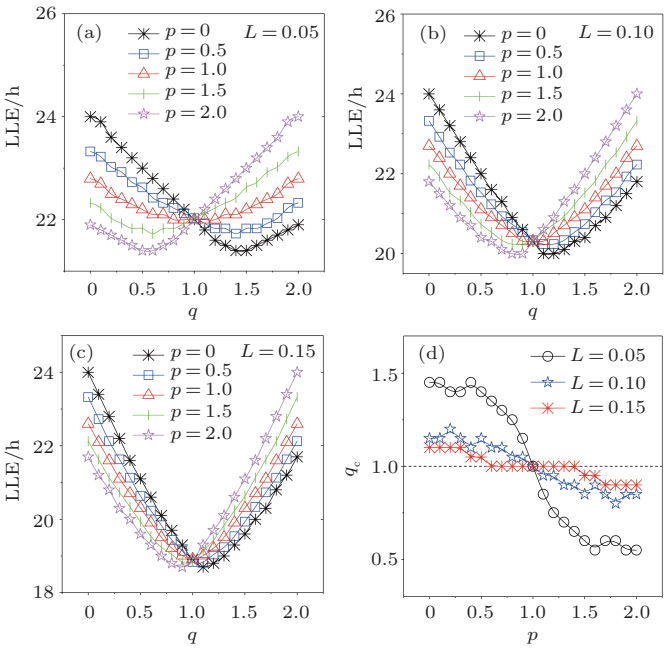


Fig. 3. The effect of the sensitivity q on the lower limit entrainment (LLE) with $G = 0.05$. The parameter L is 0.05, 0.1, and 0.15 in panels (a)–(c), respectively. The relationship of the LLE to q is parabolic-like for each case of p in panels (a)–(c). In panel (d), the relationship of the trough q_c to p is shown. Note that larger LLE corresponds to smaller entrainment range. The dashed line indicates the line of $q_c = 1$ in panel (d).

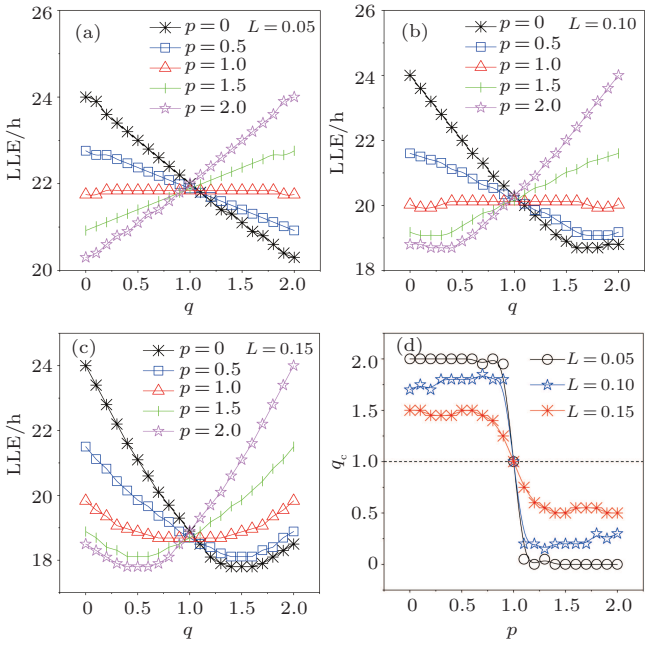


Fig. 4. The effect of the sensitivity q on the lower limit entrainment (LLE) with $G=0.15$. The parameter L is 0.05, 0.1, and 0.15 in panels (a)–(c), respectively. The relationship of the LLE to q is shown for each case of p in panels (a)–(c). In panel (d), the relationship of the trough q_c to p is shown. Note that larger LLE corresponds to smaller entrainment range. The dashed line indicates the line of $q_c=1$ in panel (d).

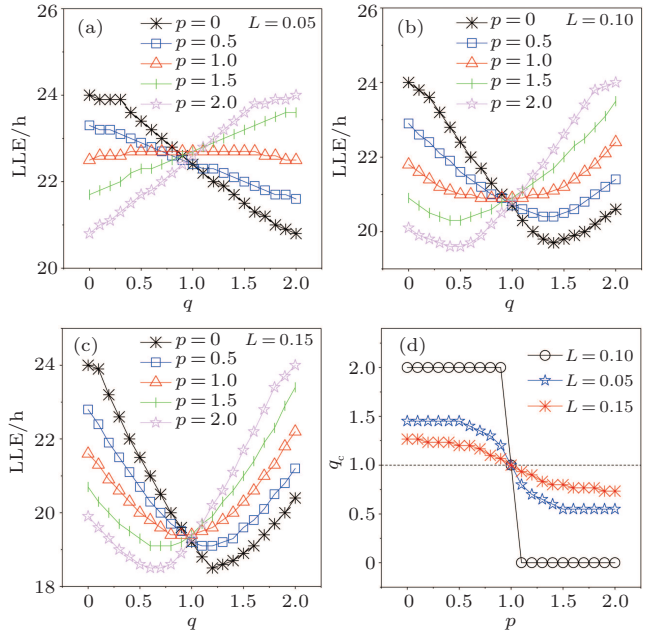


Fig. 5. The effect of the sensitivity q on the lower limit entrainment (LLE) when the intrinsic periods of the neurons are nonidentical (the standard deviation is $\beta=0.03$). The parameter L is 0.05, 0.1, and 0.15 in panels (a)–(c), respectively. The relationship of the LLE to q is monotonous for cases of $p\neq 1$ in panel (a), and is parabolic-like for each case of p in panel (b) or panel (c). In panel (d), the relationship of the trough q_c to p is shown. The number of neurons are $N=100$ and the coupling strength is $G=0.1$. Note that larger LLE corresponds to smaller entrainment range. The dashed line indicates the line of $q_c=1$ in panel (d).

Therefore, from Fig. 2 to Fig. 4, we observe that the parabolic relationship exists, and the value of trough q_c is closer to 1, if G is smaller than L, *i.e.*, the influence on the SCN neurons from the other neurons is smaller than the light-information.

The SCN neurons are nonidentical in the intrinsic periods.[33] We examine whether the main results are affected by this nonidentity. Figure 5 shows the relationship of the LLE to the sensitivity q when the standard deviation is $\beta=0.03$. It is evident that the relationship is not altered qualitatively, compared with Fig. 2. Therefore, the nonidentity does not influence the relationship, qualitatively.

4. Analytical results

For simplicity, we let N be 2, *i.e.*, one oscillator represents the first group and the other represents the second group. Equation (1) is reduced to

$$\begin{aligned}
\dot{x}_1 &= \gamma x_1(a-r_1)-\frac{2y_1\pi}{\tau}+\frac{x_1+x_2}{2}G_1,\\
&\quad +L_1\sin(\Omega t),\\
\dot{y}_1 &= \gamma y_1(a-r_1)+\frac{2x_1\pi}{\tau},\\
\dot{x}_2 &= \gamma x_2(a-r_2)-\frac{2y_2\pi}{\tau}+\frac{x_1+x_2}{2}G_2,\\
&\quad +L_2\sin(\Omega t),\\
\dot{y}_2 &= \gamma y_2(a-r_2)+\frac{2x_2\pi}{\tau},
\end{aligned}\tag{3}$$

where the mean field F is the term $(x_1+x_2)/2$, $G_{1,2}=g_{1,2}G$, and $L_{1,2}=l_{1,2}L$. For convenience, equation (3) is transformed from Cartesian Coordinates to Polar Coordinates. Let $x_1=r_1\cos\theta_1$, $y_1=r_1\sin\theta_1$, $x_2=r_2\cos\theta_2$, $y_2=r_2\sin\theta_2$. Substituting them into Eq. (3), we obtain

$$\begin{aligned}
\dot{r}_1 &= \gamma r_1(a-r_1)+(r_1\cos^2\theta_1+r_2\cos\theta_1\cos\theta_2)\frac{G_1}{2}\\
&\quad +L_1\sin(\Omega t)\cos\theta_1,\\
\dot{\theta}_1 &= \omega-(r_1\cos\theta_1\sin\theta_1+r_2\cos\theta_2\sin\theta_1)\frac{G_1}{2r_1}\\
&\quad -\frac{L_1}{r_1}\sin(\Omega t)\sin\theta_1,\\
\dot{r}_2 &= \gamma r_2(a-r_2)+(r_2\cos^2\theta_2+r_1\cos\theta_1\cos\theta_2)\frac{G_2}{2}\\
&\quad +L_2\sin(\Omega t)\cos\theta_2,\\
\dot{\theta}_2 &= \omega-(r_1\cos\theta_1\sin\theta_2+r_2\cos\theta_2\sin\theta_2)\frac{G_2}{2r_2}\\
&\quad -\frac{L_2}{r_2}\sin(\Omega t)\sin\theta_2.
\end{aligned}\tag{4}$$

When all the oscillators are entrained to the external cycle, we obtain $\dot{r}_1=0$, $\dot{r}_2=0$, $\dot{\theta}_1=\Omega$, and $\dot{\theta}_2=\Omega$. Let $\theta_1=\Omega t+\phi_1$ and $\theta_2=\Omega t+\phi_2$. Considering the averaging method developed by Krylov and Bogoliubov as used in Refs. [6,21,24,32], the alternation of ϕ has a lower time scale than Ωt. We let $\alpha=\langle\phi_2\rangle-\langle\phi_1\rangle$, and we obtain

$$\begin{aligned}
\langle\cos^2(\phi_1+\Omega t)\rangle &= \frac{1}{2},\\
\langle\cos(\phi_2+\Omega t)\cos(\phi_1+\Omega t)\rangle &= \frac{\cos\alpha}{2},
\end{aligned}$$

$$\langle\cos(\phi_1+\Omega t)\sin(\phi_1+\Omega t)\rangle = 0,$$
$$\langle\cos(\phi_2+\Omega t)\sin(\phi_1+\Omega t)\rangle = -\frac{\sin\alpha}{2}, \tag{5}$$

where $\langle\cdot\rangle$ represents the average in one circadian cycle. For simplicity, we keep the non-averaged notation r_1, r_2, ϕ_1, and ϕ_2 in the rest of the article. Substituting Eq. (5) into Eq. (4) we obtain

$$\begin{aligned}
0 &= \gamma r_1(a-r_1)+(r_1+r_2\cos\alpha)\frac{G_1}{4}\\
&\quad -\frac{L_1\sin\phi_1}{2},\\
\Omega &= \omega+\frac{r_2G_1\sin\alpha}{4r_1}-\frac{L_1\cos\phi_1}{2r_1},\\
0 &= \gamma r_2(a-r_2)+(r_1\cos\alpha+r_2)\frac{G_2}{4}\\
&\quad -\frac{L_2\sin\phi_2}{2},\\
\Omega &= \omega-\frac{r_1G_2\sin\alpha}{4r_2}-\frac{L_2\cos(\phi_1+\alpha)}{2r_2}.
\end{aligned} \tag{6}$$

When Ω is maximal, the LLE is obtained, *i.e.*, the lower limit entrainment (LLE) of the entrainment range is $\Omega_{\rm LLE}$ in frequency domain. Let $G=(G_1+G_2)/2$ and $L=(L_1+L_2)/2$. Without losing generality, we assume $G_1\le G_2$. The analytical results of $G_1>G_2$ are symmetrical to the analytical results of $G_1\le G_2$. From the second and fourth equations of Eq. (6), Ω depends on the coupling terms $C_1=(r_2G_1\sin\alpha)/4r_1$ and $C_2=-(r_1G_2\sin\alpha)/4r_2$, and the light terms $D_1=-(L_1\cos\phi_1)/2r_1$ and $D_2=-(L_2\cos(\phi_1+\alpha))/2r_2$.

Generally speaking, $\Omega_{\rm LLE}$ depends on the slower oscillator with smaller Ω. Mathematically, $\Omega_{\rm LLE}$ of the SCN is achieved through the interplay between the coupling terms and light terms. The light terms are positive which contributes to $\Omega_{\rm LLE}$. ϕ_1 and $\phi_1+\alpha$ reflect the "absorption efficiency" of the light information. When $\phi_1=\phi_1+\alpha=\pi$, where α is zero, the efficiency is perfect. However, the value of α may not be zero which depends on the coupling term. The coupling term influences $\Omega_{\rm LLE}$ through the phase difference α. If α is zero, both C_1 and C_2 are zero. If α is not zero, one of C_1 and C_2 is positive and the other is negative. In the following discussions, we will discuss the influence of $G_{1,2}$ and $L_{1,2}$ on $\Omega_{\rm LLE}$, where $G_1=pG$, $G_2=(2-p)G$, $L_1=qL$, and $L_2=(2-q)L$, under two limited conditions.

4.1. The case of $G\gg L$

If the coupling is very large ($G\gg L$, such as in Fig. 4(a)), the two oscillators are in phase, and the phase difference α is a small value. Therefore, equation (6) is reduced to

$$\begin{aligned}
0 &= \gamma r_1(a-r_1)+(r_1+r_2)\frac{G_1}{4}\\
&\quad -\frac{L_1\sin\phi_1}{2},\\
\Omega &= \omega+\frac{r_2G_1\alpha}{4r_1}-\frac{L_1\cos\phi_1}{2r_1},\\
0 &= \gamma r_2(a-r_2)+(r_1+r_2)\frac{G_2}{4}\\
&\quad -\frac{L_2\sin\phi_1}{2},\\
\Omega &= \omega-\frac{r_1G_2\alpha}{4r_2}-\frac{L_2\cos\phi_1}{2r_2}.
\end{aligned} \tag{7}$$

In order to achieve $\Omega_{\rm LLE}$, the light term should be positive and maximum. Therefore, $\cos\phi_1$ is equal to -1, and equation (7) is simplified as

$$\begin{aligned}
0 &= \gamma r_1(a-r_1)+(r_1+r_2)\frac{G_1}{4},\\
\Omega_{\rm LLE} &= \omega+\frac{r_2G_1\alpha}{4r_1}+\frac{L_1}{2r_1},\\
0 &= \gamma r_2(a-r_2)+(r_1+r_2)\frac{G_2}{4},\\
\Omega_{\rm LLE} &= \omega-\frac{r_1G_2\alpha}{4r_2}+\frac{L_2}{2r_2}.
\end{aligned} \tag{8}$$

If $G_1=G_2=G$, *i.e.*, $p=1$, the coupling is symmetrical, and the amplitudes are identical from the first and third equations of Eq. (8) which are $r_1=r_2=R=a+G/2\gamma$. Accordingly, we obtain

$$\begin{aligned}
\Omega_{\rm LLE} &= \omega+\frac{G\alpha}{4}+\frac{pL}{2R},\\
\Omega_{\rm LLE} &= \omega-\frac{G\alpha}{4}+\frac{(2-p)L}{2R}.
\end{aligned} \tag{9}$$

Adding the two equations of Eq. (9), we obtain $\Omega_{\rm LLE}=\omega+L/2R$. Therefore, $\Omega_{\rm LLE}$ is a constant which is independent of q. This finding proves that the value of LLE is independent of q in the case of $p=1$ in Figs. 2(a) and 4(a).

If $G_1=0$, *i.e.*, $G_2=2G$ and $p=0$, equation (8) is reduced to

$$\begin{aligned}
0 &= \gamma r_1(a-r_1),\\
\Omega_{\rm LLE} &= \omega+\frac{L_1}{2r_1},\\
0 &= \gamma r_2(a-r_2)+(r_1+r_2)\frac{G}{2},\\
\Omega_{\rm LLE} &= \omega-\frac{r_1G\alpha}{2r_2}+\frac{L_2}{2r_2}.
\end{aligned} \tag{10}$$

Then, we obtain

$$\begin{aligned}
r_1 &= a,\\
\Omega_{\rm LLE} &= \omega+\frac{qL}{2a},\\
r_2 &= R_2=\frac{R+\sqrt{R^2+2GR/\gamma^2}}{2},\\
\Omega_{\rm LLE} &= \omega-\frac{aG\alpha}{2R_2}+\frac{(2-q)L}{2R_2}=\omega+\frac{qL}{2a},
\end{aligned} \tag{11}$$

where $R=a+G/2\gamma$ and $\alpha=(qR_2+2a-aq)/a^2GL$. It is visible that the relationship of $\Omega_{\rm LLE}$ to q is positive. Hence, the minimum of LLE or maximum of $\Omega_{\rm LLE}$ is obtained, when q is equal to its up limited value, *i.e.*, 2. This finding is consistent with the case of $p=0$ in Figs. 2(a) and 4(a).

4.2. The case of $G \ll L$

If $G \ll L$, the contribution of the coupling terms C_1 and C_2 to $\Omega_{\rm LLE}$ is a smaller term, compared to the light term. Let $C_1 = \delta_1$ and $C_2 = \delta_2$, where $\delta_{1,2}$ is a small term. Then the second and fourth equations of Eq. (6) can be written as

$$\Omega = \omega + \delta_1 - \frac{qL\cos\phi_1}{2r_1},$$
$$\Omega = \omega + \delta_2 - \frac{(2-q)L\cos(\phi_1+\alpha)}{2r_2}. \quad (12)$$

In order to obtain the maximal absorption efficiency of the light information, ϕ_1 and $\phi_1 + \alpha$ should be close to π. Because $\Omega_{\rm LLE}$ depends on the slower oscillator, $\Omega_{\rm LLE}$ mainly depends on the smaller light terms, *i.e.*, $\Omega_{\rm LLE}$ depends on the smaller value of q and $2-q$. If $q \leq 1$, *i.e.*, $q < 2-q$, the relationship of $\Omega_{\rm LLE}$ to q is positive ($\Omega_{\rm LLE} = \omega + \delta_1 + qL/2r_1$); and if $q > 1$, *i.e.*, $q > 2-q$, the relationship of $\Omega_{\rm LLE}$ to q is negative ($\Omega_{\rm LLE} = \omega + \delta_2 + (2-q)L/2r_2$). Therefore, the relationship is parabolic-like, and the maximum value of $\Omega_{\rm LLE}$ is obtained when $q = q_{\rm c} = 1$, which is independent of p. With the increase of G, the dependence of $\Omega_{\rm LLE}$ on the light terms decreases. Lager value of G is, further from 1 the value of $q_{\rm c}$ is. This finding is consistent with Fig. 3(c).

Combined the analytical results of the two limited cases of $G \gg L$ and $G \ll L$, we conclude that in the case of $G \gg L$, $q_{\rm c} = 2$ for $p < 1$, and in the case of $G \ll L$, $q_{\rm c} = 1$ for $p < 1$. This implies that if G is around L, $q_{\rm c}$ is between 1 and 2, and with the increase of L or the decrease of G, $q_{\rm c}$ decreases in the range of 2 to 1. The cases of $p > 1$ are symmetrical to the cases $p < 1$, *i.e.*, in the case of $G \gg L$, $q_{\rm c} = 1$ for $p > 1$, and in the case of $G \ll L$, $q_{\rm c} = 2$ for $p > 1$.

5. Conclusion and discussion

In the present study, we examined the relationship of the entrainment range (represented by the LLE) to the sensitivity (q) to the photic information, where $q \neq 1$ represents there exists difference of sensitivity between the VL and the DM. We found that the relationship depends on the coupling strength. In particular, when the coupling strength (G) is much smaller than the light intensity (L), the relationship is parabolic-like, and the maximum of the entrainment range is obtained when there is no difference ($q = 1$). This relationship is independent of the direction of the coupling (represented by p). When the coupling strength is much larger than the light intensity, the relationship is monotonically decreasing or increasing if there is directed coupling ($p \neq 1$), and the maximum of the entrainment range is obtained when the difference is the largest ($q = 2$ for $p < 1$ and $q = 0$ for $p > 1$). When the coupling strength is close to the sensitive strength, the relationship is parabolic-like if there is directed coupling ($p \neq 1$), and the maximum of the entrainment range is obtained when the difference is moderate ($1 < q < 2$ for $p < 1$ and $0 < q < 1$ for $p > 1$).

In a recent experiment, both the VL neurons and the DM neurons are sensitive to light information, and the sensitive strength to the light information for the VL neurons is larger than the DM neurons.[19] However, the benefits of the difference in the sensitive strength are unknown so far. In the present study, we found that this difference may lead to large entrainment range which reflects the flexibility of the SCN to the external light–dark cycle. Our finding may provide an explanation for the exitance of the difference in the sensitivity to light-information, as well as shed light on how to increase the flexibility of the SCN represented by widening the entrainment range.

For simplicity, the SCN network is assumed to be an all-to-all network represented by the mean-field, and no noise or stochasticity is considered in the circadian signaling in the present study. Additionally, the Poincaré model is a genetic model which is oversimplification. In the future, it is worth rebuilding a more realistic model for the SCN, *i.e.*, a Goodwin model,[34] where the noise in the circadian signaling,[35–37] the amplitude difference between the neurons,[38] and the network structure, such as a small-world network, a scale-free network, and a two-layer network[39–43] are considered.

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