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Author

Wang, DeLiang

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Modeling Global Synchrony in the Visual Cortex by Locally Coupled Neural Oscillators[1]

DeLiang Wang

Laboratory of AI Research, Department of Computer and Information Science
and Center for Cognitive Science, The Ohio State University
Columbus, OH 43210-1277, USA
dwang@cis.ohio-state.edu

Abstract

A fundamental aspect of perception is to bind spatially separate sensory features, essential for object identification, segmentation of different objects, and figure/ground segregation. Theoretical considerations and neurophysiological findings point to the temporal correlation of feature detectors as a binding mechanism. In particular, it has been demonstrated that the cat visual cortex exhibits 40-60 Hz stimulus-dependent oscillations, and synchronization exists in spatially remote columns (up to 7 mm) which reflects global stimulus properties (Gray et al., 1989; Eckhorn et al., 1988). What neural mechanisms underlie this global synchrony? Many neural models thus proposed end up relying on global connections, leading to the question of whether lateral connections alone can produce remote synchronization. With a formulation different from the frequently used phase model, we find that locally coupled neural oscillators can indeed yield global synchrony. The model employs a previously suggested mechanism that the efficacy of the connections is allowed to change on a fast time scale. Based on the known connectivity of the visual cortex, the model outputs closely resemble the experimental findings. This model lays a computational foundation for Gestalt perceptual grouping.

Introduction

Since the discovery of stimulus-driven oscillations and long-range synchronization in the cortical areas of 17 and 18 of cats (Gray et al., 1989; Eckhorn et al., 1988), many theoretical attempts have been made to interpret the remarkable phenomenon of global phase locking with no phase shift (Sompolinsky et al., 1990; König & Schillen, 1991). Others have employed computational characteristics of temporal oscillations for solving problems of pattern segmentation and figure/ground segregation (von der Malsburg, 1981; von der Malsburg & Schneider, 1986; Sporns et al., 1991), and associative memory (Wang et al., 1990). Despite intensive studies, it remains unknown whether a network of locally coupled oscillators can yield global synchronization. A frequently used scheme is the phase model which represents each oscillator by a sole phase variable and describes mutual coupling by an odd periodic function such as *sine*. Characteristics of the systems of coupled phase models have been analyzed in applied mathematics and theoretical physics literature (Cohen et al., 1982; Kuramoto, 1984). It has been generally agreed that while global coupling readily yields phase locking, a system with only local coupling cannot generate global synchrony except in the homogeneous case as explained later. The application of such models to analyzing the phase locking in the visual cortex is in part responsible for the prevailing opinion that the phenomenon can only be explained by long-range projections. The view, however, is not in good accord with the anatomical data that the longest mutual connections is about 3 mm in the cat visual cortex (Gilbert & Wiesel, 1989). Based on plausible neural mechanisms, we here report a new model that can demonstrate global synchrony based on only local coupling in a network of neural oscillators.

Model Description

As the building block, the model of a single oscillator is defined in the simplest form as a feedback loop between an excitatory unit and an inhibitory unit (Fig. 1A):

$$\frac{dx_i}{dt} = -x_i + g_x(x_i - \beta y_i + S_i + I_i + \rho) \tag{1a}$$
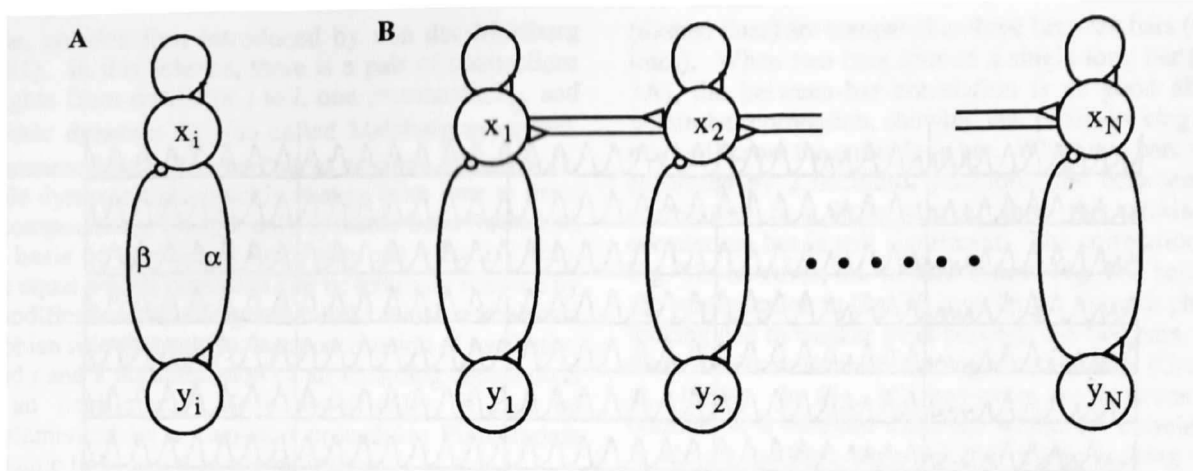
$$\frac{dy_i}{dt} = -\lambda y_i + g_y(\alpha x_i) \tag{1b}$$

Fig. 1. (A) Basic oscillator model formed by a feedback loop between an excitatory unit x_i and an inhibitory unit y_i. α and β are mutual connection strengths. (B) A chain of N oscillators. Little triangles indicate excitatory connections, and little circles inhibitory connections.

$$g_r(v) = \frac{1}{1+\exp[-(v-\theta_r)/T]}, \quad r \in \{x, y\} \quad (1c)$$

where α and β are coupling parameters between the two units. S_i represents inputs from the other oscillators and I_i represents external stimulation. λ is a decay parameter, and ρ denotes the amplitude of a Gaussian noise term. $g_r(v)$ is a sigmoid gain function with threshold θ_r, where $r \in \{x, y\}$, and parameter T. Eq. 1 is essentially a simplification of the system proposed by Wilson and Cowan (1972), and it has been shown that the system produces oscillations within a wide range of parameters. The oscillator model can be biologically interpreted as a mean field approximation to a network of excitatory and inhibitory neurons.

Weak coupling between oscillators (S_i is relatively small) does not disrupt the oscillatory behaviors of individual oscillators. To study the properties of a network of oscillators, first a chain of N oscillators is constructed with only neighboring coupling between excitatory units, as shown in Fig. 1B. The coupling is defined as

$$S_i = \begin{cases} W(x_{i-1} + x_{i+1}) & \text{if } 1 < i < N \\ 2W\,x_2 & \text{if } i = 1 \\ 2W\,x_{N-1} & \text{if } i = N \end{cases} \quad (2)$$

Where W is a connection weight. Remarkably, with uniform external input and random values for x_i and y_i (namely random phases) initially, the chain is synchronized after an initial period of "chaotic" transitions. Fig. 2 presents a simulation with $N = 30$. Notice that there is small phase differences at the

beginning when nearly stable limit cycles were reached, but the differences diminish as time went on. We note that the longer a chain, the longer is the "chaotic" transition or the longer it takes to reach phase locking. The time to reach the phase-locking stage is also related to the overall strength of coupling (W in Eq. 2). The stronger is the overall coupling, the shorter it takes to get to phase-locking.

A chain of oscillators using the phase model has been extensively studied for modeling swimming behaviors in fish. Cohen et al. (1982) noted that phase-locking can be reached with a chain of identical oscillators. However, phase-locking cannot be produced if there is no homogeneous input to the entire chain, contradicting the experimental conditions of Gray et al (1989). But, as will be clear later, our model of the oscillator system does not suffer from this problem.

Eq. 2 is not a necessary condition for phase-locking. Let us call an oscillator active if it receives an external input. We observed that in a system defined by Eq. 1, as long as the overall weights of the connections converging on an active oscillator from all other active oscillators are kept a constant, phase-locking occurs. This condition is called *the equal weight condition*. Eq. 2 is a special case of this condition. Although we are not able to prove that the equal weight condition ensures phase locking, it is quite straightforward to see that once the system reaches phase locking, synchrony will be stable. This is because each oscillator in Eq. 1 will be identical after the system reaches phase locking due to the same input S_i. Positive coupling serves to drive the oscillators close to each other in phase and it can also correct small discrepancies among the phases of the oscillators.

The equal weight condition is easily achieved if one allows connection weights to be modified on a fast time
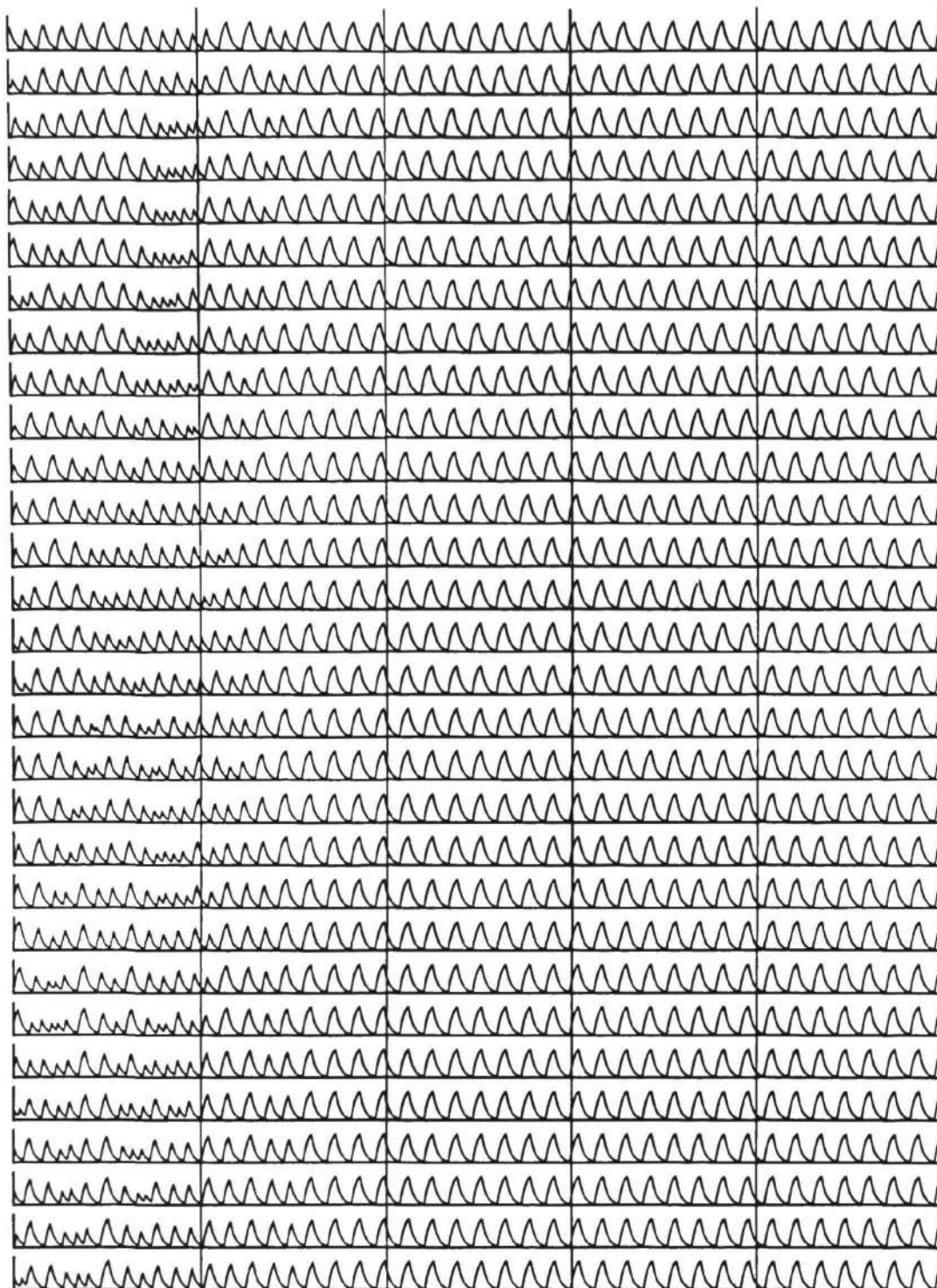
Fig. 2. Synchrony in a chain of oscillators. The input $I_i = 0.8$, and the initial values $x_i(0)$ and $y_i(0)$ were randomly generated within the range $[0, 0.5]$. The height of the ordinate of each oscillator is 1. $W = 0.625$ and $N = 30$. Other parameters $\alpha = 0.2$; $\beta = 2.5$; $\lambda = 1.0$; $\rho = 0.01$; $\theta_x = 0.6$; $\theta_y = 0.15$; $T = 0.025$. 20,000 integration steps. Vertical lines are drawn to help identify phase relations among the oscillators.

scale, an idea first introduced by von der Malsburg (1981). In this scheme, there is a pair of connections weights from oscillator j to i, one permanent T_{ij}, and another dynamic J_{ij} (so called Malsburg synapses). Permanent links reflect hardwired structure of a network, while dynamic links quickly change from time to time. In computations, though, only dynamic links formed on the basis of permanent links play the effective role. The equal weight condition can be naturally realized by a modification rule of dynamic links which combines a Hebbian rule that emphasizes coactivation of oscillators i and j and a normalization of all incoming connections to an oscillator. More specifically, it can be implemented by a two-step procedure: First update dynamic links and then normalization:

$$\Delta J_{ij} = \delta T_{ij} h(x_i) h(x_j) \tag{3a}$$

$$J_{ij} = \gamma (J_{ij} + \Delta J_{ij}) / [1 + \sum_k (J_{ik} + \Delta J_{ik})] \tag{3b}$$

where δ and γ are parameters, and function $h(x)$ measures whether x is active. It is here simply defined as $h(x) = 1$ if $<x>$ is greater than a constant and $h(x) = 0$ otherwise, where the angular bracket $<x>$ stands for temporal averaging of the activity x.

With introduction of fast changing synapses, the equal weight condition in Eq. 2 can now be reached by dynamics in Eq. 3 from a normal condition $S_i = W(x_{i-1} + x_{i+1})$, $1 \le i \le N$, and $x_0 = x_{N+1} = 0$ defined for permanent links.

Modeling Cortical Oscillations

With the above analysis, we now simulate the experiments of Gray et al. with a two-dimensional layer of 10x24 oscillators. The oscillator layer is constructed such that each oscillator laterally connects to its 8 nearest neighbors, 16 second nearest neighbors, and 24 third nearest neighbors. Each oscillator is assumed to represent an entire receptive field. The permanent coupling strengths are isotropic and fall off with distance. This kind of lateral connections is present in the primary visual cortex in the form of horizontal connections (Gilbert & Wiesel, 1989). Proper dynamic connections are formed according to Eq. 3. Following the experimental configurations, Fig. 3 presents the model response to two light bars corresponding to 2x7 oscillators separated by 0, 2, and 4 oscillator positions. Oscillators under the bars were uniformly stimulated while other oscillators received no input. Cross-correlations were computed for two oscillators within a bar and between the bars and then normalized for each trial. The upper panels of Fig.3 show stimulus configurations, and the lower panels present the correlograms. The cross-correlations within a bar

(dashed lines) are compared to those between bars (solid lines). When two bars formed a single long bar (Fig. 3A), the between-bar correlation is as good as the within-bar correlation, showing that phase-locking was reached across the entire long bar. When two bars were separated by 2 oscillator positions, the between-bar correlation is a little weaker than the within-bar correlation, but is still significant. The correlations in Fig. 3B, however, are weaker than in Fig. 3A, because the configuration in Fig. 3B took longer to reach phase-locking due to weaker links between the two bars. All these results well match the experimental data (Gray et al., 1989). In Fig. 3C, however, the between-bar correlation is minimal while the within-bar correlation is almost perfect, showing that phase-locking was readily reached within each bar but there was no phase relationship between the two bars. Note that, in this case, there was no direct link between the two bars.

The conduction delays between oscillators have been neglected in the above modeling, because the delays resulting from neighboring projections are generally much smaller than the cycle periods of the oscillators. Introducing some delays in the horizontal connections does not necessarily yield phase shift, as one might expect, since neighboring oscillators are mutually connected and they receive external input simultaneously. Our preliminary observations show that up to 0.5 ms delay (assuming 40 Hz oscillations) in neighboring connections of a chain of 15 oscillators does not prevent the chain from reaching synchronous oscillations.

The simulation results demonstrate that the visual cortex with its own lateral (horizontal) connections is capable of producing phase-locking of stimulus-driven oscillations, without resort to a global phase coordinator, all-to-all connections (Sompolinsky et al. 1990), or *adhoc* phase relations among oscillators (König & Schillen, 1991). The results provide sound computational foundations for the argument that phase-locking of oscillations is accomplished by cortico-cortical connections, which is consistent with more recent experimental findings that phase-locking can occur between the striate cortex and the extrastriate cortex, between the two striate cortices of the two brain hemispheres (Engel et al., 1992). In the simulations, as mentioned earlier, the longer a light bar, the longer it takes to reach phase-locking. Thus, if a single bar is too long, the time it takes to form phase synchrony will exceed the duration of stimulation with moving stimuli, and no phase locking can possibly be observed. This provides an explanation why no phase locking was found when two recording sites were separated too far away (8-12 mm, see Gray et al., 1989). Corresponding to Fig. 2C, we also predict that if the gap between two light bars is too long (3 mm according to Gilbert & Wiesel, 1989), no phase locking will occur across the two sites stimulated by the two bars.
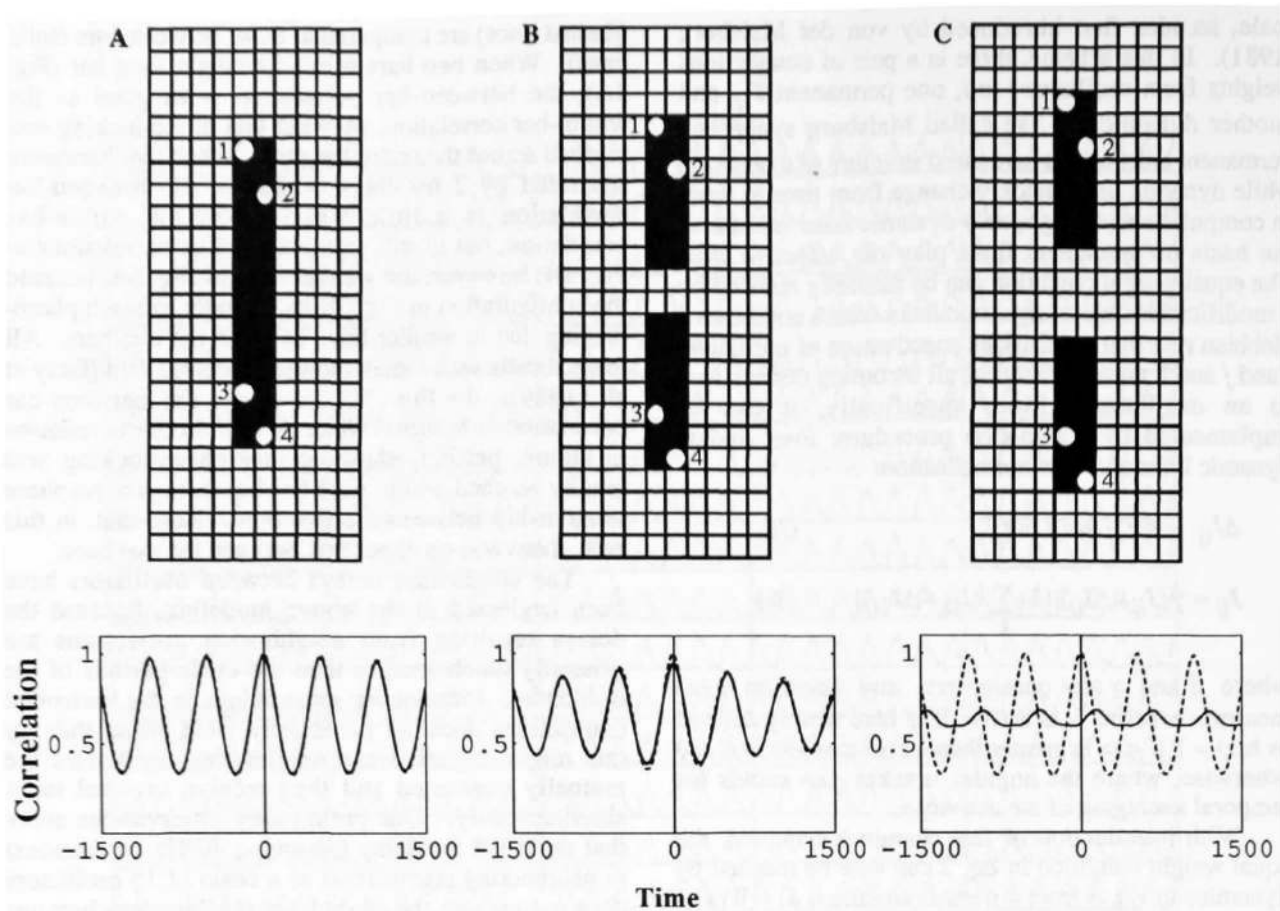
Fig. 3. Cross-correlation within and between two bars in a two-dimensional layer of locally coupled oscillators. The ratio of the coupling strengths of nearest, second nearest, and third nearest neighbors is 2:1.6:1 respectively. The overall connection strength of each oscillator is normalized to 1.25. (A) The two bars form a single long bar. (B) The two bars are separated by two oscillator positions. (C) The two bars are separated by 4 positions. The dashed lines are the normalized cross-correlation within (1-2, 3-4) and the solid lines between (1-3) the two bars. The average of 10 simulations is shown as in the experiments of Gray et al. (1989). The oscillators under the bars received external input $I_i = 0.8$, and the remaining oscillators received no external input. The initial values $x_i(0)$ and $y_i(0)$ were randomly generated within the range [0, 0.5]. The rest of the parameters are the same as in Fig. 2. Cross-correlations were computed for a time interval of 10,000 integration steps after omitting the initial 3,000 steps.

Discussion

Temporal correlation promises to provide a conceptual framework for object segmentation and figure/ground segregation (von der Malsburg, 1981; von der Malsburg & Schneider, 1986; Sporns et al., 1991). However, there is a significant obstacle to apply this idea if synchrony can only be produced with long-range full connections as in associative memory models or with a global phase coordinator (they are computationally equivalent). Long-range connections would lead to indiscriminate synchronization with a uniform structure, contrary to the Gestalt laws of perceptual grouping that emphasizes spatial and temporal relationships of the objects. To overcome this problem, the segmentation network would have to bias toward individual configurations, and the network would have to (somehow) encode individual configurations through learning or *adhoc* network configurations. Segmentation would be confused with object recognition, thus facing the similar challenges of invariant recognition, etc. To this end, segmentation would lead to the same dilemma that temporal correlation was supposedly introduced for a rescue. Notice that, although segmentation and recognition have some interactions, they are two distinct processes and segmentation is supposed to occur earlier in the visual processing than recognition.

We believe that the mechanism elucidated here provides a way out of this predicament. Sensory

segmentation can now be accomplished based on general architectures with connections only in neighboring units, the importance of which has been emphasized (von der Malsburg, 1988). The two-dimensional array of Fig. 3 can readily serve for segmentation based on connectedness and proximity, two of the most important Gestalt grouping principles. Our previous work demonstrated that oscillator groups connected by inhibitory links tend to desynchronize from each other (anti-phase locking, see Wang et al., 1990). We expect that with introduction of directional sensitivity and inhibitory projections, the present mechanism can significantly enhance the computational power of neural networks for sensory processing, and more importantly, perhaps, the understanding of neural mechanisms underlying Gestalt principles of perception.

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