The role of multi-area interactions for the computation of apparent motion

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A R T I C L E   I N F O
Article history:
Received 9 September 2009
Revised 10 March 2010
Accepted 11 March 2010
Available online 18 March 2010

Keywords:
Neuronal ring model
Apparent motion
Voltage sensitive dyes
Visual cortex

A B S T R A C T
Apparent motion (AM) is a robust visual illusion, in which fast displays of static objects in successively different positions elicit the perception of object motion. Neurons in higher order areas 21 and 19 compute object motion under such conditions and send feedback to early visual areas 18 and 17, which is instrumental in eliciting computation of motion in those very areas. To explore the computational dynamics of AM, we made a neural field model consisting of two one-dimensional rings of simple neurons expressing firing rates, one for areas 17/18 and one for areas 19/21. The model neurons, without any orientation or direction selectivity, computed apparent motion for the range of space-timings of stimuli associated with short- and long-range AM in humans. The computation of long-range AM in 17/18 required two model areas and the presence of feedback and conduction/computation delays between those areas. As in the in vivo experiments of long-range AM, the stationary stimuli were initially mapped as stationary in model area 17/18, but after the feedback also these lower areas computed AM. The dynamics of the two-area network produces short-range and long-range apparent motion for a large range of feedback strengths and a small range of lateral excitation near the bifurcation to an amplitude instability. The computation of AM in higher order areas was due to the neurons in these areas having large receptive fields as a consequence of divergent feed-forward connectivity. This implies that these areas compute long-range AM when early areas 17 and 18 do not, and therefore higher order areas must enslave lower order areas to compute the same, if the whole network is to arrive at a coherent perceptual solution.

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Introduction

Nowadays many people watch TV, movies, video displays and computer animations, often without realizing that these media only use static images. What creates the perception of visual motion from these displays is the combination of fast displays of the static objects in successively different positions. As no real physical motion occurs, the percept of object motion is an illusion, termed apparent motion. Whereas the experimental conditions for producing apparent motion have been known for more than a century (Exner, 1875; Wertheimer, 1912), the reason why the brain interprets motion from static images presented with successive spatial shifts has only partly been uncovered by recent physiological studies. The illusion of AM comes in two forms. One is short-range AM for which the distance between the successive object positions is maximally two degrees. The other is long-range apparent motion for which the distance is larger. Short-range AM has psychophysical properties distinct from long-range AM (Kolers, 1964). There are physiological studies of the primary visual area, area 17, that could be interpreted as showing single neurons being able to encode short-range AM (Baker and Cynader, 1986; van Wezel et al., 1997; Conway and Livingstone, 2003). Whether this is indeed the case or whether the short-range AM is rather a network property of area 17 is an open question (Anderson et al., 1999; Warren et al., 2004). From physiological studies of the spiking activity in visual areas associated with long-range AM, the conclusion is that more than one visual area is necessary to produce visual apparent motion. First, neurons in the primary visual area, area 17, react to long-range AM speeds only up to $8^\circ\text{s}^{-1}$, but neurons in a higher order visual area, MT, react up to $40^\circ\text{s}^{-1}$ (Newsome et al., 1986). As humans and monkeys can perceive AM when the apparent speed is up to $40^\circ\text{s}^{-1}$, at least one visual area higher in the processing hierarchy than area 17 seems necessary for the computation of apparent motion. Higher order areas actually do participate in the computation of AM in monkeys (Merchant et al., 2004) and in humans (Zhou et al., 2003; Muckli et al., 2002).

There have been several theoretical attempts to explain how the brain computes apparent motion, but only a few experiments on the underlying neurophysiology of long-range AM and only a few attempts to explain how long-range AM could be computed (Newsome et al., 1986; Series et al., 2002; Merchant et al., 2004; Ahmed et al., 2008). Ahmed et al. (2008) concluded that at least two visual areas participated in the computation of AM and that feedback from higher order areas 19/21 to lower areas 17/18 was instrumental for the computation of long-range AM in 17/18.
The study of Ahmed et al. (2008) provided some details of the dynamic interactions between four visual areas under conditions perceived as AM in humans. Ahmed et al. (2008) showed small squares, briefly flashed, at successive positions along the vertical meridian of the visual field to anesthetized ferrets (Fig. 1A). When shown at the vertical meridian, an object maps at only two locations in the four visual areas: at the border between areas 17 and 18 as stationary objects (Fig. 1B, C) and at the border between areas 19 and 21 (Roland et al., 2006, Fig. 1H). Ahmed et al. (2008) showed that net excitation propagated from the lower flashed object mapping to the mapping of the higher flashed object first along the 19/21 border and after feedback also along the 17/18 border (Fig. 1D). After this feedback the neurons fired in between the stationary maps (Fig. 1E, F, G).

The Ahmed et al. (2008) paper did not provide a reason for why the 19/21 neurons start the excitation of the cortical site of the next object position in the first place. One suggestion was that the neurons in areas 19 and 21 respond well to motion and have larger receptive fields compared to the 17/18 neurons (Manger et al., 2002; Philipp et al., 2006). The larger receptive fields of area 19 and 21 neurons may arise from overlapping feed-forward axonal connections from areas 17 and 18. The larger receptive fields imply that even small objects flashed as much as 7 degrees apart may, in areas 19 and 21, induce neurons in between the mapping sites to fire. As the areas 19 and 21 have retinotopically ordered feedback axons to areas 18 and 17 (Cantone et al., 2005, 2006), the firing of the 19/21 neurons initiated by the offset of the first object can be transmitted as a feedback to area 17/18.

As the stimuli in the Ahmed et al. (2008) paper were mapped along the 17/18 border and along the 19/21, we constructed a simple model of the first visual areas, 17/18 and of higher order visual areas 19/21. The two model areas are interconnected with retinotopically organized feed-forward and feedback connections (Cantone et al., 2005, 2006). We examine the hypotheses (1) whether short-range AM can be computed by the neurons in the primary visual area 17 only; (2) whether two interconnected areas are necessary for the computation of long-range AM. In a theoretical framework, using neural field models, we investigate the dynamical regimes in which the two-area system shows a dynamics consistent with the two forms of AM, short-range AM and long-range AM. Finally, we compare the results with electrophysiological and psychophysical data. Although very short-range AM under a special dynamic regime can be computed by the network in area 17, we suggest that the only computational way of achieving long-range apparent motion is with a system of at least two coupled neural field networks corresponding to two different brain areas.

Materials and methods

We consider a model of the mutually interacting dynamics between two visual areas of the ferret brain, namely area 17/18 and area 19/21. The dynamics of the spiking neurons in these areas can be captured in a system of nonlinear coupled differential equations which describe the evolution of the average firing rate of each population (mean-field reduction). The temporal dynamics of the firing rates of the neuronal populations can be qualitatively captured via a system of first order differential equations of the Wilson-Cowan-type (Wilson and Cowan, 1973; Dayan and Abbott, 2001; Renart et al., 2003; La Camera et al., 2004). Furthermore, we incorporate in the model the fact that the encoding of a visual stimulation in the visual cortex is distributed along many populations in both areas, each population being selective to a specific spatial localization. More concretely, for each area, the model consists of a one-dimensional ring of neuronal populations. This is a common assumption in one-dimensional neural field models of the visual cortex (see Ben-Yishai et al., 1995, and Hansel and Sompolinsky, 1998, for a thorough argumentation). The main idea is that one assumes periodic conditions, so that the main variable can be considered an angle. Then all functions of the main variable will be periodic functions with period 2π. The position of the neurons in the ring (the polar angle θ, always in radians) indicates the specific location to which the population is maximally sensitive. The polar angle θ is linearly related to the visual angle as π/4 radians on the ring corresponds to 7.8° in the field of view.

Here, we consider two coupled one-dimensional neural field networks, one corresponding to the area 17/18 border and the other to the area 19/21 border. Fig. 2 shows the schematic architecture of the model.

Thus, we get a simple neuronal field model of spike rate neurons arranged in two interconnected one-dimensional rings to exploit the computational dynamics of apparent motion. In this way we preserve the retinotopic organization and the connectivity within and between the visual areas, reducing the anatomical organization while maintaining the essence of the underlying dynamics. The axonal delays are also preserved. The main idea is to tune the connectivity dynamics close to an amplitude instability region in state space, such that the two-ring network computes apparent motion. In the literature this instability is referred to as a Touring instability. In this bifurcation region, the activity bumps persist somewhat after the stimulation, boosted by the excitatory feedback and to some extent the lateral excitation. In the Results section we will show that this mechanism in fact computes short- and long-range apparent motion.

Specifically, each network consists of a one-dimensional ring model (i.e. we adopt periodic boundary conditions), where the polar angle indexes the spatial position of the neuron population. Each network includes excitatory and inhibitory neurons. Nevertheless, a ring model consisting of mutually connected excitatory and inhibitory neurons can be reduced (Hansel and Sompolinsky, 1998) to a ring model considering only excitatory neurons, but assuming a pattern of connectivity which includes in negative synaptic connections the inhibitory communication to the excitatory neurons. We make the following assumptions in designing the model: the strength of the within-area interactions depends on the distances between the connected neuronal populations; the lateral connectivity in area 19/21 is wider than in area 17/18; the feed-forward and feedback connections between neuronal populations in both area 17/18 and area 19/21 are divergent. We take a realistic delay of 4 ms in the feed-forward connections from area 17/18 to area 19/21, and a delay of 8 ms in the feedback connections from area 19/21 to area 17/18 (Papaioannou and Roland, unpublished results). We also include in area 17/18 narrow receptive fields encoding the retinal input signal. Finally, we assume isotropic mapping of the retina on the 17/18 ring.

We adopt here a neural field approach, assuming that the spatial index is continuous. We denote with r(θ, t) the population rate activity of the unit in area 17/18 at location θ and at time t. Similarly, we denote with r′(θ, t) the population activity in area 19/21. The time evolution of the neuronal activation in both areas can be described by the following system of coupled differential equations (Hansel and Sompolinsky, 1998):

\[ \begin{align*}
\tau \frac{dr(0, t)}{dt} &= -r(0, t) + f \left( \int_0^\tau d\omega \left( \sum_{n=1}^\infty \omega(W(\theta-\tilde{\theta})r(\tilde{\theta}, t-t_2)) + \xi_n(t) \right) \right) \\
\tau \frac{dr(\pi, t)}{dt} &= -r(\pi, t) + f \left( \int_0^\pi d\omega \left( \sum_{n=1}^\infty \omega(W(\theta-\tilde{\theta})r(\tilde{\theta}, t-t_1)) + \xi_n(t) \right) \right)
\end{align*} \]
where the local intracortical connectivity functions $f, f'$ are defined by

\[ f(\theta) = \frac{2\pi}{X} (-J_0 + J_2 e^{-\theta^2/X}) \]  
\[ f'(\theta) = \frac{2\pi}{X} (-J_0 + J_2 e^{-\theta^2/X}) \]

where $J_0$ and $J_2$ denote the strength of the local inhibition and excitation, respectively. The intercortical connectivity functions $W, W'$ are defined by

\[ W(0) = W'(0) = \frac{\pi}{\alpha} e^{-\theta^2/\alpha^2} \]

In Eqs. (3)–(5), $\lambda, X$ refer to the spread of the local connectivity in areas 17/18 and 19/21, respectively, whereas $\alpha$ refers to the spread of the connections between those areas. The external stimulation is taken as

\[ h_{ext}(\theta - \theta_0) = c \left( 1 - 2b + 2he^{-\lambda(\theta - \theta_0)^2/2} \right) \]

where $c$ denotes the contrast, $b$ the angular anisotropy, $\mu$ the spread of the sensorial input and $\theta_0$ the position at which the external stimulus is presented.

The transfer response function $f(\cdot)$ is a semi-linear gain function defined as

\[ f(x) = 0 \text{ for } x \leq T \]
\[ f(x) = \gamma(x - T) \text{ for } x > T \]

The parameter $T$ is the threshold and $\gamma$ the gain factor of the function. This is the function used in Ben-Yishai et al. (1995) and Hansel and Sompolinsky (1998), reflecting the experimental finding that neural responses exhibit a sharp threshold below which they vanish. Fluctuations are modeled via an additive Gaussian noise term denoted by $\xi$. Here $\langle \xi(t) \xi(t') \rangle = \beta^2 \delta(t - t')$, where the brackets $\langle \cdot \rangle$ denote the average over stochastic random variables. This noise term represents finite-size effects that arise due to the finite number $N$ of neurons in the populations.

In this paper, we took $c = 0.2$, $b = 0.5$, $J_0 = 0.2$, $\lambda = 0.3$, $X = 0.6$, $\alpha = 0.4$, $\mu = 0.2$, $\beta = 0.02$, $\gamma = 1$, $T = 0$ (Ben-Yishai et al., 1995; Hansel and Sompolinsky, 1998) and the intercortical delays were $\tau_1 = 4$ ms and $\tau_2 = 8$ ms, in accordance with experimental results (Papaoannou and Roland, unpublished). For the discretization of the equations we took 640 populations in each ring.

As already mentioned and further detailed in the Results section, the working point of the whole network has to be adjusted so that the system works at the edge of an amplitude instability bifurcation. In order to find that edge, we simulated the noise-free system defined above (i.e. with $\beta = 0$) for different values of the local strength of the excitation, $J_0$, and the feedback strength from area 19/21 to area 17/18, $f_b$. The simulations set a stimulation at a fixed position ($\theta = 0$ for 500 ms, and then we observe the evolution of the bump for long times. The amplitude instability corresponds to the cases where the height of the bump starts to diverge. Fig. 3 shows the results of these simulations. The green region corresponds to the region of instability. For our simulation we choose the point marked on the figure, $J_2 = 0.9$ and $f_b = 0.16$.

**Results**

The visual cortical areas of ferrets have a relatively complex layer and connectivity pattern. Nevertheless, the dynamics of neurons here can be captured by abstract models that express the activity of these neurons as a function of space and time. In particular, we will consider, for the description of the activity in each brain area, a neural field model which essentially describes the average spiking rate of a population of neurons over short periods of time. A neural field model not only describes the dynamical evolution of the spiking rate activity at one particular neuronal population, but also considers a spatially distributed extension of the evoked cortical activity, so that a continuous variable is also used for indexing the spatial dimension. The motion of net excitation and firing within an area can be captured by a one-dimensional spatial neural field model. The Ahmed et al. (2008) experiments were done with apparent motion along the vertical meridian of the field of view. As a consequence, the objects were mapped along the cytoarchitectural borders between area 17/18 and 19/21, respectively (as opposed to four mappings of the object, one in each area if the objects were displayed...
Fig. 3. Bifurcation diagram of the ring model system with the two neural fields. The green region denotes the amplitude instability. In this region the firing rates in the bumps increase without bound. The white domain is for most parts a stable domain in which the bumps of activity just develop at the stimulated/input zones and disappears when the stimulation ceases. This would correspond to the appearance of two independent objects. However, in a zone close to the bifurcation border, AM is produced by the model elsewhere in the field of view). For this reason, two one-dimensional model areas, mutually connected by feed-forward/feedback connections, would suffice to capture the dynamics in the Ahmed et al. experiments. In the Materials and methods section, all the equations underlying the model dynamics are specified.

The behavior of the model required for achieving apparent motion is such that the two coupled areas should be able to sustain a bump of activity, elicited by a brief presented stimulus, long enough so that another brief presented stimulus in a nearby position after a short enough time is able to provoke a movement of the bump to the new position. The bump of increased firing rate would then correspond to the mapping of the object. Precisely this smooth movement of the bump of statistically increased firing rate between the two object mapping positions would correspond to apparent motion, as will be explained in detail below and seen in Fig. 4A and B. We found that a condition for having apparent motion is that the recurrent excitation due to the feed-forward and feedback communication between the two networks be strong enough to sustain the bump of activity for a while, but not so strong that the bump gets unstable, or even stable after the disappearance of the object. In dynamical terms, this means that the system worked at the edge of an amplitude instability bifurcation.

The overall behavior of the model is summarized in Fig. 3. The figure shows the bifurcation diagram of the system, and localizes the limits of the amplitude instability bifurcation as a function of two parameters, namely the strength of the feedback and the strength of the local excitation. If the system is far from the bifurcation limit in the instability region (green area), then the amplitude of a bump elicited by an external stimulus increases without bound. On the other hand, if the system is far from the bifurcation limit in the stable region (white area), then a bump elicited by an external stimulus would immediately disappear when the external stimulus is withdrawn. We systematically explored the parameter region shown in Fig. 3. When we tune the system, by varying $f_b$ and $J_2$, to operate at the edge of the bifurcation (in the white area), it is able to reproduce the dynamics associated with apparent motion as in the experiments. While apparent motion can be computed for many parameter points at the border of the bifurcation, we highlight in the figure the parameter point chosen for the simulations further illustrated in the paper ($J_2 = 0.9$ and $f_b = 0.16$).

In the first experiment we show the dynamics of areas 17/18 and 19/21 for a presentation of the stimulus at two different positions, with a space-timing such that apparent motion is induced. Specifically we show at time $t = 0$ ms a stimulus at a position $\theta = 0$ for 100 ms, and after a 100 ms gap without stimulation, i.e. at $t = 200$ ms, we present an identical stimulus at the position $\theta = \pi/4$. $\pi/4$ in our calibration equals 7.8° in the field of view.

Fig. 4A shows the evolution of the spatial firing rate of both areas for different times. The times shown are 100, 200, 210, 220, 230, and 250 ms. The figure clearly shows the motion of both bumps (area 17/18, bottom, and area 19/21, top) toward the second cortical position of the object.

Fig. 4B shows the evolution of the spatial activity bump for the case where the temporal gap between the object presentations increases from 100 ms to 400 ms, i.e. the second presentation, in this case, is applied at the same $\theta = \pi/4$ but at $t = 500$ ms. In this case one would expect that the object presentations are perceived as the sequential appearance of the object in two successive positions with no apparent
motion. This is exactly what the model computes: the bump elicited by the first object after 100 ms of stimulation remains in position and decreases in amplitude over the next 300 ms until almost disappearing. After the presentation of the object in the second position at 500 ms, a new bump of increased firing rate appears at the second object mapping position, growing in amplitude (firing rate) up to $t = 600$ ms. The times shown are 100, 200, 300, 500, 520, 530, 550, and 600 ms. Note that in both Fig. 4A and B there is an overlap of the 19/21 increased firing rates between the two mapping sites already from the time when the first input arrives from the 17/18 network.

A complementary way for visualizing the movement of the bump under different stimulus conditions is by plotting the evolution of the position of the maximum of the bump (maximal firing rate) as a function of time. We will show for simplicity just the evolution of the bump in area 17/18.

Fig. 5A shows this for the conditions mentioned above, i.e. apparent motion when the object is flashed at its second position at $t = 200$ ms and no apparent motion when it is flashed at the second position at $t = 500$ ms. The conditions for no apparent motion give clear sharp transitions from one cortical position to the next, i.e. no gradual movement of the maximal firing rate.

We systematically changed the position of stimulus 1 and 2 input to area 17/18 ($\theta$) and measured the evolving dynamics. At small values of $\theta$, the two area ring-system produced AM for all values of $\theta$ up to $\pi/2$ equal to $15^\circ$, keeping the delay between the stimuli at 100 ms. That is, the two area system produced AM for values of $f_b = 0.051$ and $J_2 = 0.6$, corresponding to the zone near the bifurcation limit in the white area of Fig. 3. Removing the feedback totally ($f_b = 0$) removed the possibility of area 17/18 to produce AM. Only under the extreme condition of having a strong and widespread local excitation in area 17/18 ($J_2 > 1$) right at the bifurcation limit intersection with the x-axis, could the 17/18 area produce AM for $\theta < 15^\circ$, i.e. with the stimuli separated by about 1 degree. This condition, though, is very unstable for the model. So the model produced short- and long-range AM with both areas connected with feed-forward and feedback connections, and only under an extreme parameter condition could area 17/18 alone produce short-range AM.

In order to analyze the role of the feedback coming from area 19/21, Fig. 5B shows the evolution of the 17/18 maximal firing rate for delays of 100 ms and 400 ms between the flashing of the object at $\theta = 0$ and $\theta = \pi/4$ (corresponding to 7.8° apart) with and without feedback from area 19/21. The apparent motion effect is only elicited in the presence of feedback. The relevance of the timing in the feed-forward/feedback communication between area 17/18 and area 19/21 is shown in Fig. 5C where the feedback is present, but including or not the time delays in the connections. The absences of time delays destroy the apparent motion effect. The absence of feedback as well as zero delays in the feed-forward/feedback communications in the model, either singularly or in combination, always prevents the computation of apparent motion for any values of delay and distance.

The apparent motion illusion depends on the distance between and the timing of the first and second position of the object on the retina. If the distance is increased, the time interval between the two object presentations must be shortened (Korte’s law). The range of inter-stimulus interval within which AM is perceived decreases with increasing distance between the positions where the object is flashed. Furthermore, in general the object in the first position must disappear prior to or just when it is flashed again at the second position. If the delay between the stimulus onset times at the two positions is less than 25 ms, two objects will be perceived to appear simultaneously. If it is longer than 500 ms, two objects will be perceived to appear sequentially. Within these limits humans perceive apparent motion.

Fig. 5. Evolution of the maximum of the bump activity in area 17/18. (A) Apparent motion versus no-apparent motion case. (B) Apparent motion case, with and without feedback. (C) Apparent motion case, with feedback, but with and without delays between areas 17/18 and 19/21.
As not only the timing, but also the distance between the object positions affect whether apparent motion is computed by the brain or not, we systematically changed both the delays, in steps of 50 ms from 0 ms to 400 ms, and the distance between the two object positions, in steps of 1° from 1° to 14°. Here 1° and 2° would correspond to short-range apparent motion and 4° or more to long-range apparent motion. The domain within which the model produced apparent motion is shown in Fig. 6. One may see that this corresponds reasonably well with the findings of Kolers (Kolers (1964)) for humans.

As the model provides only firing rates, we compared the performance of the model to the electrophysiological results of Ahmed et al. (2008). The model neuron located in between the two stimulated sites, 7° apart on the 17/18 ring, did not fire significantly in response to either stimulus, when presented as singletons. The sum of the rate responses to the two singleton presentations is shown in blue in Fig. 7. In contrast, when object 1 and object 2 were presented at those same positions with an inter-stimulus interval of 0 ms, i.e. the first object on at 0 ms then off at 100 ms, and the second object on at 100 ms, the firing was statistically significantly higher for the neuron located in the middle between the stimulation sites (red curve, Fig. 7). This condition of AM was identical to that used by Ahmed et al. (2008). As seen in Fig. 7, the significant firing of the model neuron started at 120 ms. This corresponds to the experimental results shown in Fig. 1F, where the firing of a multiunit is shown situated midway between the retinotopic locations of the two objects at the 17/18 area border. This unit did only fire significantly under the apparent motion condition, starting at 115 ms. Fig. 1G further shows the time interval in which all units situated in between the two retinotopic sites of the objects fired statistically more under the AM condition than the sum of the spikes from the conditions when the objects were presented as singletons.

The relation between the feedback strength and the intracortical lateral excitatory connectivity is shown in the state-space diagram (Fig. 3). Note that AM is computed by the dual ring model in a narrow zone close to the bifurcation, i.e. for a large range of feedback strengths. When the feedback strength is zero, the model could compute AM, but only at an extreme lateral excitatory connectivity. In the state space diagram this corresponds to the small corner just when the bifurcation border crosses the x-axis.

Discussion

We constructed a very simple neuronal field model with spike-rate neurons arranged in two interconnected one-dimensional rings to exploit the computational dynamics of apparent motion. These types of models preserve in a simple way the retinotopic organization and the connectivity within and between cortical areas, as well as the axonal delays structure, but they reduce the anatomical organization in such a way that the essence of the underlying dynamics is preserved. The two-ring network computed apparent motion when the network was close to an amplitude instability region (Fig. 3). The network computed short- and long-range apparent motion for the ranges of stimulus delays and stimulus distances producing AM in humans. Whereas short-range apparent motion under particular extreme lateral spreading excitation could be computed by one area, the computation of AM needed two areas coupled with feed-forward and feedback connections with realistic conduction delays as a minimum requirement. The spike-rates of the network were in accordance with that observed in in vivo computations of AM (Ahmed et al. (2008)).

We used delays of 4 ms and 8 ms, respectively, for the feed-forward and feedback connections, in accordance with the experimentally observed values from ferret visual areas 17/18 and 19/21 (Papaioannou and Roland, unpublished results). The feed-forward connectivity was modeled to give a receptive field of <7 for 17/18 area neurons and 12° or 15° in 19/21 area neurons. These receptive field sizes are in accordance with the values for the center of the visual field reported by Manger et al. (2002) and Cantone et al. (2005) for the 19/21 area neurons. For a stimulus presented in the center of the field of view, the receptive field size in area 17/18 is twice the reported value, but a receptive field size at the 17/18 border at 5° eccentricity would be in accordance with published values (Manger et al., 2002; Cantone et al., 2005).

Series et al. (2002) presented a more detailed model of apparent motion computation by using three levels: lateral geniculate nucleus, the primary visual area V1, and the motion sensitive area MT connected by feed-forward connections. This model, and other models with only a single area, incorporated orientation selectivity and directional selectivity of the neurons (Grossberg and Rudd, 1992; Francis and Grossberg, 1996; Baloch and Grossberg, 1997; Series et al., 2002, 2003). Our model uses, for the neural field, simple firing rate neurons with no assumptions of orientation and directional sensitivity. Despite the simplicity of the ring model, it computes short-range and long-range apparent motion over the combinations of distance and delays expected from human psychophysics (Kolers, 1964; Braddick, 1980; Anstis and Mather, 1985;
Chubb and Sperling, 1988). Thus orientation selectivity and directional selectivity are not necessary to compute apparent motion.

When the retina is still, objects moving in the field of view are invariably mapped as increases in the population membrane potentials and firing rates moving over cortical areas 17, 18, 19, and 21 in retinotopic coordinates (Harvey et al., 2009). In our study we were able to find a condition in which two stationary objects, displayed in quick sequence, after feedback from areas 19/21 were mapped as two moving increases in firing rates and population membrane potentials in retinotopic coordinates in the ferret areas 17/18 and 19/21 (Ahmed et al., 2008). When areas 17/18 were stimulated with two stationary stimuli (“objects”) with identical distance and delay, the stationary stimuli, after feedback were mapped as two moving increases in the firing rates in retinotopic coordinates in our two-ring model of areas 17/18 and 19/21. Invariably this stimulation with moving objects elicits AM in humans. Although it remains to be demonstrated that perception of AM in humans is always associated with a mapping by increased firing rates or increased population membrane potentials moving in the direction of AM over the cortex, this is a reasonable hypothesis. The full range of conditions resulting in the perception of AM in humans has not yet been fully explored in invasive experiments in animals. However, for a range of distances and delays giving rise to AM in humans, our two-ring model, after feedback produces moving increases in firing rates in the 19/21 as well as the 17/18 ring.

The ring model computed apparent motion with some overlap in firing in the 17/18 area. This overlap, however, was not instrumental for the computation of apparent motion, because AM could be computed even without it. In contrast, zero delay between the areas, the absence of feedback and absence of overlap of receptive fields or of lateral excitation in area 19/21 were the three factors precluding the computation of AM. The necessity of delays in communication between areas is interesting as conduction delays usually complicate computations to the extent that authors tend to ignore their presence (Jirsa, 2004; Deco et al., 2008). The prediction arising from this is that axonal conduction delays of visual information between areas are necessary for the generation of AM in lower order visual areas. Thus AM would not exist there if the cortico-cortical axonal conduction speed approached infinity. Higher order areas with retinotopic organization might still be able to produce AM if the receptive fields of the neurons overlapped considerably, as in area 19/21 in our case. This will create a discrepancy in computation among the higher and lower order areas that would not be resolved. In the case that no area has any overlap of the spiking to the two sequential stimuli, all fast sequential displays of objects in different positions should be perceived as separate static objects displayed in distinct positions.

Let us remark on the need of two coupled areas for achieving the desired dynamics. A single area model (i.e. one ring model) can of course be tuned at the edge of an amplitude bifurcation instability, so that short-range apparent motion dynamics could appear (corresponding to the crossing of the bifurcation border with the x-axis in Fig. 3). Nevertheless, the robustness of this dynamics is extremely limited because the only variable regulating that is the strength of the local excitatory spread. The spatial spread of the local firing was fundamental for the generation of the movement of the bump, and limits strongly the range where the new stimulation has to appear. The addition of a second area is not only necessary given the experimental/simulation evidence, but also convenient from a purely computational point of view. The second area can have a much larger spatial spread of the local connectivity, so that the range of spatial positions where the second stimulus should appear in order to cause apparent motion can be more easily extended. In this context it is important to stress again the relevance of the delays in the communication between the two areas.

The fact that the model with two coupled areas is tuned at the edge of an amplitude instability for showing the desired behavior is one example more of a neuronal network that shows maximal sensitivity and dynamic range at the critical point of a phase transition (Kinouchi and Copelli, 2006). This suggests a general principle of brain processing.

In the ring model the feedback transmits the result of the computation in the higher order area 19/21, apparent motion, to area 17/18 as in the Ahmed et al. (2008) study. In area 17/18 the dynamics depends on the feedback strength and the lateral net excitation. Lateral spreading net excitation from the object mapping site is a common mechanism in lower visual areas of carnivores and primates (Grinvald et al., 1994; Slovin et al., 2002; Roland et al., 2006; Ahmed et al., 2008). As all higher order areas have larger receptive fields than do lower order areas, most likely due to the organizations of the feed-forward connections, the computations will always be different among the visual areas. Neurons in area 17 have the smallest receptive fields, which make this area initially compute stationary representations of the stimulus at two different visual locations. The feedback is then the mechanism by which the network of visual areas can enslave also early visual areas to compute AM out of stationary stimuli.

Acknowledgments

We acknowledge the support by the Spanish Research Project BFU2007-61710, and CONSOLIDER CSD2007-00012, plus the support from the Swedish Science Council K 2010-62X-09456-20-3 to P.E.R.

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