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Correspondence and requests for materials should be addressed to G.R. (e-mail: gilbert.roberts@ncl.ac.uk).

Visual synchrony affects binding and segmentation in perception

Marius Usher & Nick Donnelly

Department of Psychology, University of Kent at Canterbury, Kent CP2 7NP, UK

The visual system analyses information by decomposing complex objects into simple components (visual features) that are widely distributed across the cortex^{1,2}. When several objects are present simultaneously in the visual field, a mechanism is required to group (bind) together visual features that belong to each object and to separate (segment) them from features of other objects. An attractive scheme for binding visual features into a coherent percept consists of synchronizing the activity of their neural representations^{3–6}. If synchrony is important in binding, one would expect that binding and segmentation are facilitated by visual displays that are temporally manipulated to induce stimulus-dependent synchrony. Here we show that visual grouping is indeed facilitated when elements of one percept are presented at the same time as each other and are temporally separated (on a scale below the integration time of the visual system⁷) from elements of another percept or from background elements. Our results indicate that binding is due to a global mechanism of grouping caused by synchronous neural activation, and not to a local mechanism of motion computation.

Despite compelling neurophysiological support for the synchrony-binding hypothesis from animal studies (for reviews see refs 8, 9), the first psychophysical studies on humans that tested the effects of temporal manipulations on visual binding did not provide positive results^{10–12}. However, a new series of studies^{13–15} demonstrated that human subjects can perform texture discrimination when texture and background elements were spatially identical but presented in a different temporal phase (that is, discrimination was performed on the basis of temporal information only). Although this might be the first psychophysical confirmation of the use of temporal synchrony for visual binding in humans, an alternative explanation needs to be ruled out. Texture discrimination can be computed either on the basis of grouping (of the elements within each texture separately) or on the basis of local gradients at texture boundaries¹⁶. In this case, one could argue that gradient computations at boundaries generate a (possibly implicit) motion signal that

partially mediates the effect. To rule out such an explanation, we used two types of experiment that are different from texture discrimination in an attempt to, first, engage global grouping and segmentation processes but not local boundary computations, second, demonstrate the existence of a grouping mechanism that is independent of the computation of motion (even if only implicit), and third, show that grouping by temporal asynchrony interacts with spatial information, thus excluding a statistical decision based on two independent sources of information.

The first set of experiments tested grouping within a symmetric square lattice display (Fig. 1a), which is typically perceived as either rows or columns^{17,18}. Three types of display were randomly presented in a mixed design (Fig. 1a), and subjects were required to perform a forced choice about their perception of the lattice (rows or columns). In condition one, all the elements were flashed on and off together (synchronous trials); in condition two, at each successive time cycle alternating rows of the lattice were flashed on together (asynchronous-row trials); in condition three, alternating columns were flashed on together (asynchronous-column trials). The temporal asynchrony was 16 ms, which corresponds to a total time cycle of 32 ms. This asynchrony resulted in a perfectly steady lattice percept with no flicker or motion reported by subjects.

As expected, decisions in synchronous trials were evenly divided between rows and columns (because of the symmetry of the square lattice). However, during asynchronous displays the temporal structure affected subjects' perception. The probability of choosing rows or columns consistent with the temporal manipulation is shown in Fig. 1b, and is much larger than would be expected by chance (for one sample $t[7] = 35.3$, $P < 0.001$), although display times were so short that eye movements could not be made and the temporal asynchrony was much lower than that which can be detected in temporal discrimination tasks using similar displays¹⁹.

A second interesting result is that the probability of correct detection in asynchronous trials increased with contrast ($F(1, 7) = 34.76$, $P < 0.01$) but decreased with increasing display duration (Fig. 1b; $F(2, 14) = 6.84$, $P < 0.01$). Although the effect of display duration is opposite to that predicted by Bloch's law, it can be explained by a simple model showing that short displays (resulting in transient activation) are more distinct than longer displays (which engage a steady activation pattern), as shown in Fig. 1d. Finally, we found a strong trend towards better performance when using circles rather than crosses in the display ($F(1, 7) = 5.3$, $P = 0.055$). This might indicate that the impact of stimulus-induced synchrony is larger when internally induced synchronization does not dominate; internal synchronization is likely to be stronger when using crosses than when using non-orientated elements (circles) because of the lateral connections between cells with similar orientation preference within the visual cortex^{20,21}. A similar finding has been reported¹⁴ showing that the tendency to choose a target based on temporal grouping is diminished when its percept conflicts with another percept based on spatial grouping.

Although the subjects reported no motion in the lattice display, we attempted to rule out the possibility that these results are based on an implicit motion computation (vertical oscillatory 'motion' of rows and horizontal oscillatory 'motion' of columns). Another group of subjects performed an experiment in which the same displays were used but in which the subjects were required to make a

Table 1 Stimulus-response matrix for the 3AFC task

| | Response R | Response C | Response S |
|------------|-------------|-------------|-------------|
| Stimulus R | 0.62 (0.07) | 0.15 (0.04) | 0.23 (0.04) |
| Stimulus C | 0.15 (0.04) | 0.68 (0.07) | 0.18 (0.04) |
| Stimulus S | 0.25 (0.04) | 0.29 (0.05) | 0.46 (0.07) |
| Average | 0.34 | 0.37 | 0.29 |

Results are means \pm s.e.m. of response probabilities for eight subjects. The three stimuli, R (rows), C (columns) and S (synchronous), are shown in rows, and the three responses in columns. The values are normalized to the fractions of responses generated for each stimulus, and therefore the numbers in each row sum to unity.

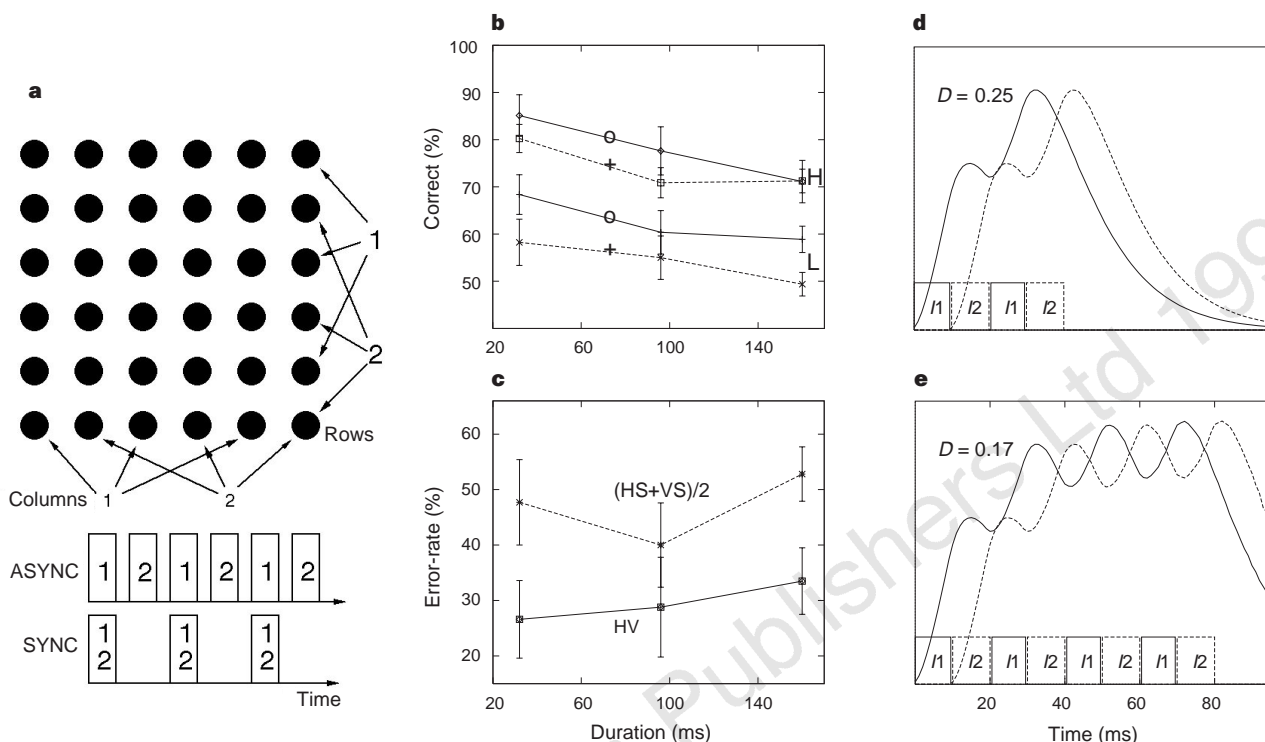


Figure 1 Effects of temporal structure on grouping. **a**, Display used in experiment 1. A square lattice of elements (either filled circles, as shown here, or crosses) was presented for a period of variable duration in one of three conditions (rows, columns and synchronous). The elements of the lattice appear relatively bright on a grey background; two levels of element brightness were used with relative contrast $((L_1 - L_2)/(L_1 + L_2))$ of 0.3 and 0.07. The temporal structure of the display involved three types of trial, randomized within a mixed design. First, synchronous trials took place in which all the elements were flashed together for a 16-ms time interval, followed by a blank screen in the following 16-ms interval. This 32-ms cycle was repeated for a period of total duration 32, 96 or 160 ms (SYNC (synchronous) condition). Second, asynchronous row trials, and third, asynchronous column trials were used. In these trials, successive rows or columns of elements, respectively, were flashed in successive 16-ms intervals (ASYNC (asynchronous) condition). Subjects were required to make a forced choice decision about their perception of the lattice. Auditory feedback was given after

three-alternative forced choice (3AFC) between row (or 'moving' vertically), column (or 'moving' horizontally) and synchronous (or 'not moving') responses. If motion was the mechanism mediating performance in this task, one would expect more confusions between types of asynchronous ('moving') display than between synchronous and asynchronous displays, as studies of motion perception have shown that the threshold for discriminating between two orthogonal directions is higher than the threshold for detecting motion²² (the thresholds are close to equal only for directions with angles larger than 120°). Subjects performed much better than chance ($P_{correct} = 0.59 \pm 0.06$ (s.e.m.); $P_{chance} = 0.33$; one sample $t(7) = 4.03$, $P < 0.005$) (Fig. 1c). A comparison of error types between conditions shows that subjects were much more likely to confuse synchronous ('non-moving') displays with either of the asynchronous ('moving') displays (HS, VS) than to confuse different asynchronous displays (HV) ($F(1, 7) = 21.28$, $P < 0.01$). Furthermore, the stimulus-response matrix (averaged across subjects and durations, Table 1) shows that the tendency to confuse synchronous and asynchronous stimuli is not the result of a moderate response bias towards generating row or column responses relative to synchronous responses overall (average response probabilities are 0.34 and 0.37 versus 0.29 respectively). When either row or column displays were presented, and errors

responses inconsistent with the stimulus manipulation. **b**, Probability of choosing rows/columns (eight subjects) consistent with the stimulus manipulation (for asynchronous trials) as a function of the total display time, two levels of contrast (L, low, or H, high) and the two types of element (circles and crosses); chance level is 50%. **c**, Error rates (eight subjects) for a triple choice between rows (horizontal, H; moving up-down), columns (vertical, V; moving left-right) and static (synchronous, S). Confusions between synchronous and asynchronous-row stimuli (HS), confusions between synchronous and asynchronous-column stimuli (VS) and confusions between rows and columns (HV) are shown; chance level for errors is 66%. **d, e**, The effect of total duration on discriminability, D , of the two consecutive inputs in the ASYNC condition. Y-axis shows inputs (I_1, I_2) and activations of hypothetical visual detectors (a_1, a_2 , obtained by convolving the inputs with an alpha function, $f(t) = t \exp(-t/\tau)$, with $\tau = 10$ ms (ref. 25), for a short (**d**) and a long (**e**) display. (D is computed according to $f|a_1 - a_2|dt/f|a_1|dt$.)

made, the errors were more likely to involve synchronous responses than the opposing asynchronous response (0.23 and 0.18 relative to 0.15); this is the opposite result to that expected on the basis of a response bias alone (which should favour row/column confusions). Therefore, the pattern of confusions contradicts predictions of a motion mechanism that is better at detecting than discriminating between motions. These results indicate that grouping (in rows/columns) and not implicit motion is the mechanism responsible for the effect.

In a second type of experiment, we tested the effect of temporal asynchrony in a task that required subjects to group and detect quasicollinear line elements from a background of randomly orientated line elements in a four-alternative force choice (4AFC) task (Fig. 2a). This is not a texture discrimination task, as elements within the background are not uniformly orientated and the 'target' does not enclose a surface. Fast grouping on the basis of only spatial information has been demonstrated for such a task²³. Subjects performed much better when target and background elements were flashed cyclically and asynchronously at a time lag of 16 ms (collinear-asynchronous condition) than in the collinear-synchronous condition ($F(1, 4) = 10.6$, $P < 0.05$) (Fig. 2b). This shows that a short temporal asynchrony of 16 ms facilitates the binding of elements within the target and their segmentation from background

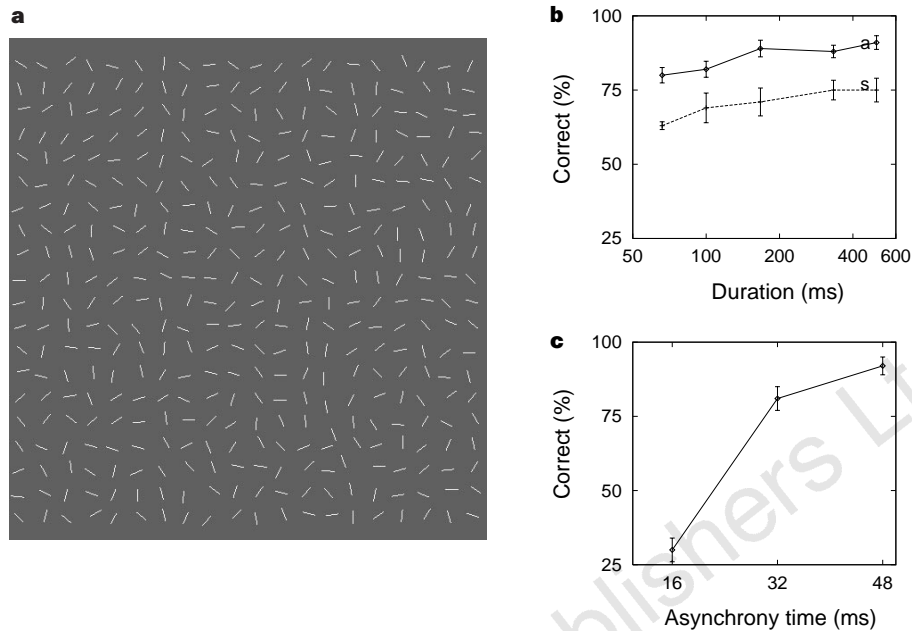


Figure 2 Effects of temporal structure on the detection of collinear target elements presented within a noisy background. **a**, Display example (the target is in the bottom right quadrant and is vertically orientated). A curved line segment is embedded within a background noise mask made of randomly orientated line elements using the algorithm described in ref. 23. The line segment is made of seven elements and appears randomly in one of the four quadrants of the display. Subjects were required to perform a 4AFC task, choosing the quadrant in which the line segment was shown. Stimuli were randomized according to the following two conditions: first, synchronous (target and background were flashed together for 16 ms, every 32 ms, as in Fig. 1a SYNC condition); and second, asynchronous (target and background were flashed in opposite phases, as in Fig. 1a ASYNC

condition). A control condition (random asynchronous) required detection for asynchronous displays when the target line elements were presented in the same positions as in the collinear condition but with their orientations randomized; under this condition the target is characterized by temporal information only. Auditory feedback was provided after incorrect responses. **b**, Probability of correct detection (five subjects) as a function of the duration of the display for two temporal structures: first, synchronous (s) and second, asynchronous (a). **c**, Probability of detecting the target against the background (ten subjects) when the orientation of the target line elements is randomized (control condition). The total display time is 200 ms, and the cycle time of the asynchrony is 16, 32 or 48 ms. In both tasks the chance level is 25%.

elements. Figure 2c shows that performance drops to chance level (25%) at the leftmost data point (one sample $t(9) = 1.83, P > 0.1$) when the same target elements (with the same spatial locations) have collinearity removed by randomizing their orientations so that they are distinguished from background only by the 16-ms asynchrony (random-asynchronous condition). As the random-asynchronous condition should provide the same motion signal as the original display (because the spatial-temporal difference between target and background elements is statistically the same), this shows that the facilitation effect is not due to an implicit motion detection (according to which some facilitation should have been found in the random-asynchronous condition).

A replication of this study, using a within-subject design (eight subjects) and increasing the temporal resolution of the display to 75 Hz (13 ms), produced similar results. For each subject, we compared performance in the collinear-asynchronous condition with the performance, P_{ind} , predicted from a multinomial model. This model was based on the independent probabilistic summation of spatial and temporal information and guessing (with chance probability 0.25, corresponding to 4AFC), computed according to: $P_{ind} = P_{spatial} + (1 - P_{spatial})P_{temporal} + 0.25(1 - P_{spatial})(1 - P_{temporal})$, where $P_{temporal}$ and $P_{spatial}$ are estimated from: $P_{random-async} = P_{temporal} + 0.25(1 - P_{temporal})$, $P_{collinear-sync} = P_{spatial} + 0.25(1 - P_{spatial})$. For each subject, the performance in the collinear-asynchronous condition was higher than that predicted on the basis of independent probabilistic summation; the average difference in response probability was 0.1 (one sample $t(7) = 7.32, P < 0.001$).

The results of the grouping in collinearity experiments indicate that the temporal information in our displays interacts with spatial information and is not used independently. This is consistent with the finding that temporal synchrony between a random set of

elements of a texture target and random elements in the background does not interfere with texture segregation on the basis of spatial features^{11,14}. A common explanation¹⁴ is that temporal grouping between elements takes place only when the target elements have compatible spatial alignments through which they can be grouped into a coherent percept (in ref. 14 grouping into a coherent percept takes place when the elements enclose a surface; in our second set of experiments it takes place when they form a continuous curve).

Our results, together with those of other studies¹³⁻¹⁵, indicate that a small temporal asynchrony, below the visual integration timescale, can have a direct effect on grouping. These results are evidence for a synchrony-binding mechanism and support previous studies that showed a failure of neural synchrony to correlate with visual binding deficits in strabismic amblyopic cats²⁴. Nevertheless, further combined psychophysical and neurophysiological studies are required to test and reveal the nature of the synchrony-binding mechanism. □

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Correspondence and requests for materials should be addressed to M.U. (e-mail: mu@ukc.ac.uk).

Inhibitory long-term potentiation underlies auditory conditioning of goldfish escape behaviour

Yoichi Oda, Keisuke Kawasaki, Masahiro Morita, Henri Korn* & Haruko Matsui

Laboratory of Neuroscience, Division of Biophysical Engineering, Graduate School of Engineering Science, Osaka University, Machikaneyama 1-3, Toyonaka, Osaka 560-8531, Japan

* Laboratoire de Biologie Cellulaire et Moléculaire, INSERM U261, Institut Pasteur, Paris, France

Long-term potentiation (LTP), the increase in synaptic strength evoked by high-frequency stimulation, is often considered to be a cellular model for learning and memory. The validity of this model depends on the assumptions that physiological stimuli can induce LTP *in vivo* and that the resulting synaptic modifications correlate with behavioural changes. However, modifiable synapses are generally embedded deep in complex circuits. In contrast, the goldfish Mauthner (M)-cell and its afferent synapses are easily accessible for electrophysiological studies, and firing of this neuron is sufficient to trigger fast escape behaviour in response to sudden stimuli^{1,2}. We have previously shown that tetanic stimulation can induce LTP of the feedforward inhibitory synapses that control the excitability of the M-cell^{3,4}. Here we report that natural sensory stimulation can induce potentiation of this inhibitory connection that resembles the LTP induced by afferent tetanization. Furthermore, comparable acoustic stimulation produced a parallel decrease in the probability of the sound-evoked escape reflex. Thus we demonstrate for the first time, to our knowledge, a behavioural role for the long-term synaptic strengthening of inhibitory synapses.

When monosynaptic excitation of the M-cell by afferents of auditory nerve (VIII)^{1,2} causes the cell to fire, a stereotyped escape reflex, or 'C-start', is initiated by activation of contralateral spinal

circuits^{1,2,5}. This predator-avoidance behaviour is under the control of a feedforward glycinergic inhibition^{2,6} (Fig. 1a). We investigated whether these connections are potentiated after repeated tones and whether the C-start is similarly modified.

We first studied inhibitory postsynaptic currents (IPSCs) evoked by nerve VIII using single-electrode voltage clamp (SEVC) in the contralateral M-cell soma (Fig. 1b), where it is uncontaminated by any excitatory response. We also assessed the underlying conductance change measured from r' , which is the ratio of amplitudes of the shunted (V') and control (V) antidromic spikes evoked by spinal stimulation^{4,7,8} (Fig. 1b; see Methods). Repeated sounds induced an LTP of the inhibitory synaptic current or IPSC (Fig. 1c). The IPSC evoked by nerve VIII reached $145 \pm 11\%$ ($P < 0.01$)

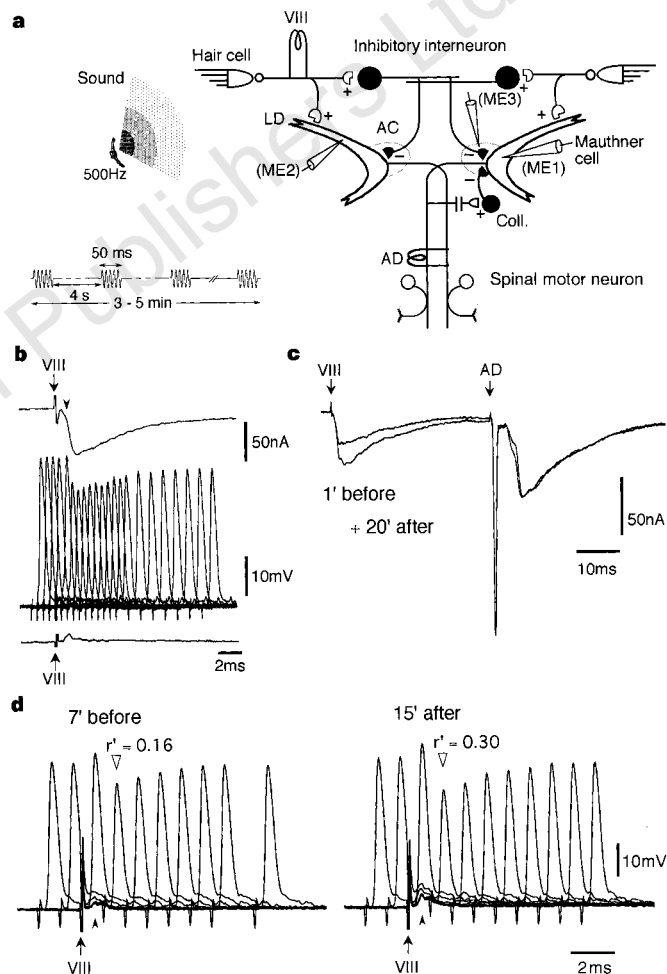


Figure 1 Induction of inhibitory LTP by sound. **a**, M-cell networks activated by sound and parameters of conditioning bursts. Nerve VIII primary fibres excite (+) the lateral dendrite (LD) of the ipsilateral M-cell and inhibitory interneurons (-). The M-cell also receives inhibition through a recurrent collateral pathway (Coll.). AD, Antidromic stimulation of the M-axon and of the recurrent pathway. ME1, ME2 and ME3: recording microelectrodes in the contralateral soma, in the ipsilateral LD, and in the axon cap (AC, dotted line). **b**, Top, average IPSC ($n = 4$) recorded at resting potential ($V_m = -81$ mV) by a single-electrode voltage clamp (SEVC), chopping frequency 20.5 KHz with a KCl microelectrode. Arrowhead, onset of IPSC. Middle, test AD spikes evoked at various intervals ($n = 3$ for each) after contralateral nerve VIII stimulation, recorded in the same cell with a KAc microelectrode. Bottom, presynaptic volley alone. **c**, IPSC evoked by nerve VIII followed by an AD spike and a subsequent collateral IPSC recorded before and after a 4 min application of repeated sounds ($n = 7$ sweeps) (SEVC, chopping frequency 18 KHz, $V_m = -77$ mV). **d**, AD spikes paired with contralateral nerve VIII stimulation as in **b**, before and after conditioning with sound bursts. Note that the time of maximum shunt (triangle) is consistent with a disynaptically evoked inhibition (diagram in **a**). Arrowhead, presynaptic volley.

