Journal of Experimental Psychology:
Human Perception and Performance
2006, Vol. 32, No. 3, 610–617

0096-1523/06/$12.00 DOI: 10.1037/0096-1523.32.3.610

Role of Gamma-Band Synchronization in Priming of Form Discrimination for Multiobject Displays

Hongjing Lu
University of California, Los Angeles

Robert G. Morrison
Xunesis

John E. Hummel
University of Illinois at Urbana–Champaign

Keith J. Holyoak
University of California, Los Angeles

Previous research has shown that synchronized flicker can facilitate detection of a single Kanizsa square. The present study investigated the role of temporally structured priming in discrimination tasks involving perceptual relations between multiple Kanizsa-type figures. Results indicate that visual information presented as temporally structured flicker in the gamma band can modulate the perception of multiple objects in a subsequent display. For judgments of both relative orientation and relative position of 2 rectangles, response time to identify and discriminate relations between the objects was consistently decreased when the vertices corresponding to distinct Kanizsa-type rectangles were primed asynchronously. Implications are discussed for models of the perception of objects and their interrelations.

Keywords: binding, neural synchrony, Kanizsa-type figure discrimination, relation coding, visual priming

Perceiving complex visual scenes entails keeping track of multiple objects and their interrelations, requiring the nervous system to solve the fundamental *binding problem* (Hummel, 1999; von der Malsburg, 1995). The binding problem arises at multiple levels of perceptual representations. To perceive the arrangement of objects in a scene, people must bind together features that compose a unified object and segregate features of distinct objects; to perceive the arrangement of parts composing a single object, people must bind together the features of individual parts and segregate features of distinct parts (Green & Hummel, 2004; Hummel & Biederman, 1992; Hummel & Stankiewicz, 1996, 1998; Stankiewicz & Hummel, 2002; Stankiewicz, Hummel, & Cooper, 1998; Thoma, Hummel & Davidoff, 2004).

One neural mechanism that may contribute to solving the binding problem exploits phase locking of firing: Neurons representing features of the same object (or part) may fire in synchrony with one another and out of synchrony with neurons representing features of other objects (or parts) in the visual field (Singer, 2004; Singer & Gray, 1995). Neurophysiological evidence suggests that the gamma band (approximately 40 Hz; range estimated at 30–80 Hz) is most likely to be involved in binding by synchrony (Eckhorn et al., 1988; Haig, Gordon, Wright, Meares, & Bahramali, 2000; König & Engel, 1995; K. H. Lee, Williams, Breakspear & Gordon, 2003; Lisman, 1998; Rodriguez et al., 1999).

Although the existence of gamma-band activity is well established (K. H. Lee et al., 2003), the hypothesis that phase locking in the gamma band serves a binding function for vision remains controversial. Electrophysiological evidence suggests that synchrony underlies feature binding for single objects, both in adults (Elliott, Herrmann, Mecklinger, & Müller, 2000) and in infants as young as 8 months (Csibra, Davis, Spratling, & Johnson, 2000). There is some psychophysical evidence that synchrony may serve as a cue to figure–ground segregation (S. H. Lee & Blake, 1999) or visual grouping (Usher & Donnelly, 1998).

Priming by Synchrony in Single-Object Displays

Elliott and Müller (1998, 2000, 2001) developed a novel priming paradigm to investigate the role of neural synchrony in binding the features of single objects in noisy displays. In their paradigm, participants must detect the presence of a Kanizsa square in a display containing many elements that could, but do not, form the corners of such a square (see Figure 1). Their critical manipulation concerned the nature of the temporal information in a *prime* display that immediately preceded the presentation of the static target display.

For example, Elliott and Müller (1998, Experiment 1) used target displays that either did or did not contain a Kanizsa square defined by four systematically oriented inducing junctions. The

---

Hongjing Lu and Keith J. Holyoak, Department of Psychology, University of California, Los Angeles; Robert G. Morrison, Xunesis, Chicago, Illinois; John E. Hummel, Department of Psychology, University of Illinois at Urbana–Champaign.

This project was made possible by funding from the International Fellowship from the American Association of University Women to Hongjing Lu, National Institute of Mental Health (NIMH) National Research Service Award MH-064244 to Robert G. Morrison, funding from Xunesis to Robert G. Morrison, and NIMH Grant 1-R03-MH072613:01A1 to Keith J. Holyoak. A preliminary report of this research was presented at the 46th Annual Meeting of the Psychonomic Society, Toronto, Ontario, Canada, November 2005.

We are grateful to Randolph Blake and Zili Liu for helpful discussions. Glyn Humphreys and Marius Usher provided valuable comments on early drafts. We thank Arun Bahl, Airom Bleicher, Lila Al-Marhoon, Jason Woods, and Poya Yaghoubian for excellent technical assistance.

Correspondence concerning this article should be addressed to Hongjing Lu, Department of Psychology, University of California, Los Angeles, CA 90095-1563. E-mail: hongjing@psych.ucla.edu

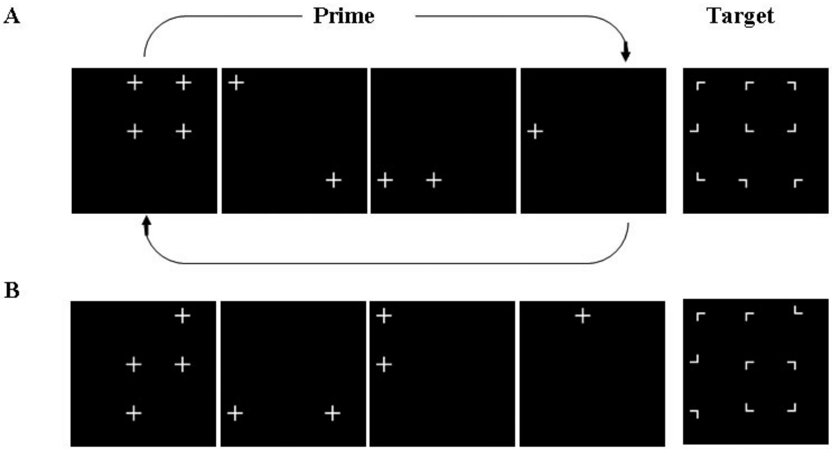

Figure 1. Experimental paradigm to study priming by synchrony in single-object displays (Elliott & Müller, 1998, 2000, 2001). A: synchrony priming; B: random priming.

grid size was 3 × 3; inducer lengths were set to low values that had been estimated to yield perception of a good square with less than .1 probability (Shipley & Kellman, 1992). Observers were required to make a yes–no discrimination to indicate whether a Kanizsa square was present. On target-absent trials, the junctions were misoriented so as not to induce a square. Observers responded by pressing one of two response buttons to indicate *yes* or *no*, and reaction times (RTs) and accuracy were measured.

On each trial, the target display was preceded by a prime consisting of four frames, each containing from one to four crosses at points on the 3 × 3 grid, cycling at a particular frequency for a duration varying from 300 to 4,800 ms. In the synchronous condition (see Figure 1A), the first frame displayed four crosses in positions corresponding to the vertices of the target Kanizsa square, whereas the other three frames had crosses at random locations. In the random condition (see Figure 1B), the crosses in all four frames were in random positions. In both conditions, across all four frames a cross appeared at each location in the grid exactly once. Elliott and Müller (1998) found that observers were able to detect the square on target-present trials more quickly and accurately when the locations of the square's four vertices were primed synchronously at the rate of 25 or 40 Hz (where the rate refers to the presentation of each individual frame in the priming stimulus). The magnitude of the priming effect was about 10 ms for 25-Hz and 40-Hz primes. Synchronous and random primes did not differ on target-absent trials; accordingly, the synchrony advantage observed for target-present trials could not be attributed to a general bias to respond "present" on synchrony-primed trials (as such a bias would have led to errors on target-absent trials). Reliable priming was not observed at presentation rates faster than 40 Hz.

Elliott and Müller (1998, Experiment 2) also performed a detection experiment to assess whether the synchronous priming effect could be attributed to observers' becoming aware of the synchronous prime. On each trial a prime was presented, and the observer was asked to press one of four keys to indicate whether one or more rectangular frames had been present, providing one of two possible levels of confidence for the decision. A signal detection analysis indicated that observers were able to reliably detect square primes at the 25-Hz presentation rate but not at 40 Hz. Overall, Elliott and Müller's findings support the hypothesis that synchronous primes in the central gamma band (40 Hz) are able to facilitate detection of ambiguous objects (Kanizsa squares) without the observer being able to detect the structure of the priming stimuli.

Elliott and Müller's (1998) demonstration that gamma-band synchronous flicker in the stimulus can influence perceptual grouping is counterintuitive. Even if the visual system in fact uses gamma-band synchronous firing to represent perceptual binding (e.g., for perceptual grouping, as in the case of Kanizsa-type figures), we would expect the visual system to impose synchronous (and asynchronous) firing on visual neurons in response to the perceptual grouping cues present in the stimulus (e.g., gestalt cues; see Hummel & Biederman, 1992). Unless gamma-band oscillations in the stimulus are common cues to perceptual grouping (which seems unlikely), there is little a priori reason to expect them to drive neural oscillations of the type that might carry binding information. Indeed, using a very different paradigm, Keele, Cohen, Ivry, Liotti, and Yee (1988) failed to show effects of stimulus-based oscillations on perceptual grouping. Nonetheless, it may be that Elliott and Müller's priming paradigm, using ambiguous stimuli lacking in strong gestalt cues, is better suited to detect subtle effects of stimulus-driven synchrony on perceptual grouping. In addition, their priming paradigm has the advantage that it tests the impact of temporal information without confounds that may arise when temporal information is combined with (potentially competing) spatial information.

Priming by Asynchrony and Synchrony in Multiobject Displays

The present experiments extend the paradigm developed by Elliott and Müller (1998, 2000, 2001) to investigate the potential role of neural synchrony and asynchrony in binding for multiobject displays. When the visual field contains features of multiple objects that enter into perceptual relations to one another (e.g., objects are of the same or different shape, or one is on top of the other), the visual system must solve the binding problem both at the level of individual objects (grouping the features of each object) and at the level of relations between objects (e.g., distinguishing separate objects to assess the relations between them; Hummel & Biederman, 1992). Such multiobject binding is a critical component of scene recognition, a task at which humans are highly skilled (see Green & Hummel, 2004).

In a multiobject display, synchrony can be manipulated both within and between objects. In the case of a display containing two objects, a prime can either synchronize all the features of both objects (e.g., if each object has four features, all eight features can be presented in synchrony with one another, a situation we term a *synchronous* prime), or it can synchronize features of each object while desynchronizing features of different objects (e.g., the eight features of two objects can be presented in two packages of four, a situation we term an *asynchronous* prime). We extend Elliott and Müller's (1998, 2000, 2001) priming paradigm to investigate the impact of both synchronous and asynchronous primes in tasks requiring discrimination of a visual relation between two ambiguous objects. As we elaborate shortly, some theories that postulate synchrony as the basis for perceptual binding (e.g., Hummel & Biederman, 1992; Hummel & Holyoak, 1997, 2003; von der Malsburg, 1994, 1995; see also Luck & Vogel, 1997) predict that, inasmuch as the participants' perceptual task requires them to explicitly compute a relation between the objects, the asynchronous prime condition should produce greater facilitation than the synchronous prime condition.

Figure 2 illustrates the basic target displays for the discrimination tasks used in the present study. Each display contained two Kanizsa-type rectangles in a 6 × 6 grid consisting of inducing junctions and distractor elements. In Experiment 2, the orientations of the rectangles could be either the same (both vertical or both horizontal; Figures 2A and 2B) or different (see Figure 2C). (Whereas in Experiment 2 we manipulated the *same-* vs. *different-orientation* relations, in Experiment 3 we manipulated the *above/below* vs. *beside* relations between the two objects.) On each trial, the target display was preceded by a prime consisting of four frames cycling at a particular frequency (generally 60 Hz) for 1.2 s (a duration in the midrange of those Elliott & Müller, 1998, showed to be effective).

In the asynchronous condition (see Figure 2A), the second and fourth frames each displayed crosses in positions that corresponded to one of the two rectangles that would appear in the target, whereas in the first and third frames random locations were marked. In the synchronous condition (see Figure 2B), the third frame displayed crosses in positions corresponding to both target rectangles, whereas the other three frames had crosses at random locations. In the random condition (see Figure 2C), the crosses in all four frames appeared in random positions.

According to the JIM model of visual binding in object recognition (Hummel, 2001; Hummel & Biederman, 1992; Hummel & Stankiewicz, 1996), multiple objects (or object parts) are represented by synchronized firing of neurons for the features of each individual object (or part), with neurons representing the features of separate objects (or parts) firing out of synchrony with one another. In particular, local interactions between units representing edge fragments and vertices in the model's first two layers (roughly analogous to neurons in visual areas V1 and V2 of the macaque) induce those units to fire in synchrony if they represent local features of the same convex geometric part, or geon (Biederman, 1987), and out of synchrony if they represent local features

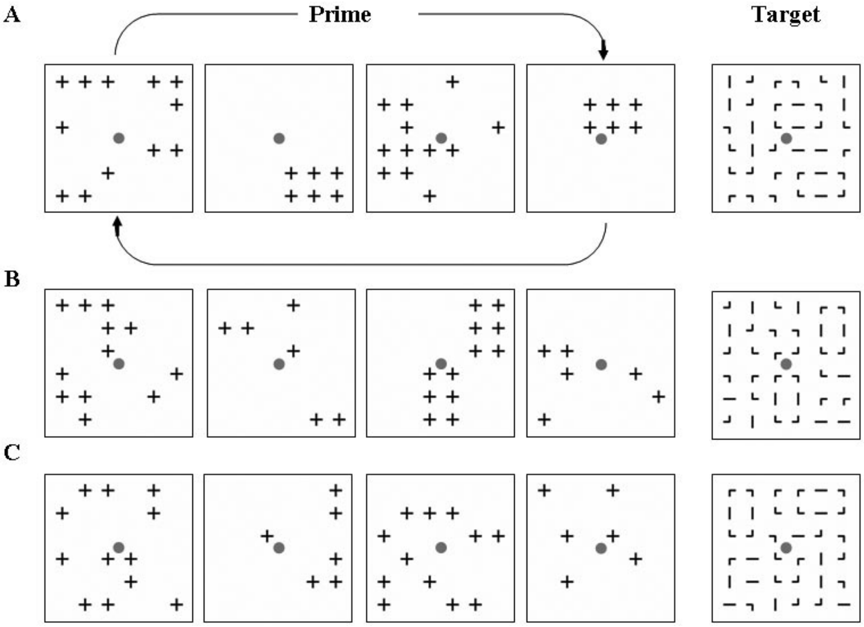

Figure 2. Basic experimental paradigm. Observers saw four priming frames, collectively forming a 6 × 6 grid, which flickered repeatedly for 1.2 s at 60 Hz. In each frame, either 12 (Frames 1 and 3) or 6 (Frames 2 and 4) of 36 possible locations were marked with a cross. A target then appeared, and observers decided whether the Kanizsa-type rectangles were oriented in the same or different directions. A: asynchronous condition, same orientation; B: synchronous condition, different orientation; C: random baseline, different orientation.

of separate geons (Hummel & Biederman, 1992; for a more recent algorithm, see Hummel, 2001). The resulting synchrony relations are carried forward into the later layers of the model and serve both to represent the binding of geon attributes and to bind geons to their interrelations (e.g., specifying whether one geon is larger than another or above another) to form geon-based sets. Geon attributes can be categorical, such as whether the geon has a straight or curved major axis, whether it has a straight or curved cross-section, and whether its sides are parallel (as in a cylinder) or nonparallel (as in a cone); geons can also be metric, such as the geon's size, location in the visual field, and orientation.

If neural timing is indeed the basis for binding features into parts and objects and if these kinds of bound representations can be primed, then, relative to the random baseline condition, the asynchronous prime should facilitate perception of the two target rectangles, reducing RT to discriminate relations between them. By contrast, although the synchronous condition should bind the features of the individual rectangles (which we would expect to facilitate perception of the objects), it may also tend to bind the two rectangles into a single unified percept. If judgments of perceptual relations between rectangles require observers to perceive the rectangles as distinct objects, synchronizing them could interfere with the comparison. In this case, the synchronous condition would yield less facilitation on the discrimination task than would the asynchronous condition. This prediction is counterintuitive, as the synchronous condition (in which the features of the two rectangles appear together at the same time) is more similar to the target display (in which the two rectangles appear together in a static display) than is either the asynchronous or the random condition.

Alternatively, it is possible that relational representations are difficult or impossible to prime subliminally (see Stankiewicz et al., 1998; Thoma et al., 2004) and that the kind of priming Elliott and Müller (1998) observed is restricted to midlevel feature grouping. In this case, we would expect to see priming of approximately equal magnitude (relative to the random control condition) in both the synchronous and the asynchronous conditions.

Experiment 1

To select a flicker rate for use in discrimination experiments, we first conducted a detection experiment (similar to that performed by Elliott & Müller, 1998) to assess observers' ability to identify primes presented at varying flicker rates. The potential priming stimulus was presented at 20 Hz (50 ms per frame), 40 Hz (25 ms per frame), or 60 Hz (16.7 ms per frame), always with a total presentation time of 1.2 s. The 40-Hz and 60-Hz frequencies fall within the accepted bounds of the gamma band, whereas the 20-Hz frequency lies below that band.

Method

Participants. The observers were 11 student volunteers at the University of California, Los Angeles (UCLA). They were graduate students and undergraduate research assistants in cognitive psychology.

Apparatus and stimuli. We presented image frames using a Macintosh G4 computer on an Apple 17-in. (43.18-cm) CRT screen. All frame elements were displayed at the center of the screen, and observers viewed the monitor at a distance of 57 cm (maintained via a chin rest) through a dark tube that abutted the computer monitor to prevent any external interference with luminance. Experiments were conducted in a dim room, with black stimulus luminance maintained at 0.75 cd/m^2 on a gray background field of 60.20 cd/m^2. We used a gray background to minimize afterimages. The resolution of the monitor was 832 × 624 pixels, with a refresh rate of 120 Hz. We used the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) to generate the stimulus and control the monitor synchronization. The prime display grid was 6 × 6 with 36 identical crosses, subtending 7° × 7° of visual angle. Each cross subtended 30′ of visual angle; the centers of adjacent crosses were separated horizontally and vertically by 1°10′ of visual angle. The line width of crosses was 3′ of visual angle.

Each prime consisted of four frames, collectively forming a 6 × 6 grid, which flickered repeatedly for 1.2 s at either 20, 40, or 60 Hz. In each frame, either 12 (Frames 1 and 3) or 6 (Frames 2 and 4) of 36 possible locations were marked with a cross. In the asynchronous condition, the locations of the two rectangles were cued in Frames 2 and 4, respectively, 180° out of phase; Frames 1 and 3 were random. In the synchronous condition, both rectangles were cued in Frame 3; the other frames were random. In the random baseline condition, all frames contained crosses at random locations. The initial frame was random in all conditions. A red fixation dot was displayed constantly, and observers were instructed to fixate on it during the entire trial.

Design and procedure. Experiment 1 consisted of one 30-min session with 480 test trials administered in three blocks, with a 2-min rest period between blocks. An equal number of trials presented asynchronous, synchronous, and random primes. Trials of all prime types and frequencies were randomly intermixed. On each trial a prime was presented, and the observer was asked to press one of four keys to indicate whether one or more rectangular frames had been present. The four keys were used to indicate two levels of confidence (*guess* or *certain*) that one or more rectangular frames were or were not present in the prime display. No feedback was given. Fifty practice trials preceded test trials.

Results and Discussion

On the basis of signal detection theory, we used the confidence data to compute the A_z measure (Dorfman & Alf, 1969). An A_z value of .50 indicates a complete lack of ability to discriminate primes with temporal structure (asynchronous or synchronous condition) from random primes (see Table 1). We calculated A_z scores for each condition for individual observers and also analyzed group means.

Analyses revealed that all 11 observers could detect asynchronous and synchronous primes at 20 Hz. Individual A_z scores were reliably greater than .50, according to a z test, and the mean A_z score for the group was also reliably greater than .50, according to a t test. For 40-Hz primes, 7 observers had above-chance A_z values for asynchronous primes, and 10 had above-chance A_z values for

Table 1
Detection of Rectangles During Flicker Priming (Experiment 1)

	Asynchronous primes		*Synchronous primes*	
Frequency (Hz)	No. detecting[a]	Mean A_z	No. detecting[a]	Mean A_z
20	11	.98[b]	11	.98[b]
40	7	.60[b]	10	.68[b]
60	2	.54	4	.55

[a] For each frequency of flicker priming, the number of observers (out of 11) reliably detecting the prime (individual A_z reliably greater than .5, $p < .05$). [b] Mean A_z reliably greater than .5, $p < .05$.

synchronous primes. Group A_z scores were reliably above chance for both types of primes presented at 20 or 40 Hz. For 60-Hz primes, only 2 observers were able to reliably detect the presence of rectangular frames in asynchronous primes, and 4 observers reliably detected them in synchronous primes. The Group A_z scores (.54 for the asynchronous condition and .55 for the synchronous condition) were not reliably greater than the chance value of .50. Note that detection of a rectangular frame does not imply that observers were able to detect the orientation of either or both primed rectangles. Accordingly, even if an occasional observer shows above-chance detection ability for 60-Hz primes, the observer may still be unaware of the orientations of the rectangles. Observers reported that 60-Hz primes appeared as unidentifiable flicker.

The results of Experiment 1 indicate that the ability to detect rectangular primes was minimal for 60-Hz presentations. Our findings contrast somewhat with those of Elliott and Müller (1998), who found that observers were unable to reliably detect squares in primes presented at 40 Hz. The stimulus display used in our study (black targets on a gray background) had a lower luminance contrast and a higher mean brightness than the displays Elliott and Müller used (white targets on a black background); across many perceptual paradigms, it has been shown that the internal effect of stimuli is proportional to stimulus contrast (Busey & Loftus, 1994). In any case, multiple procedural differences (e.g., we used larger grid sizes and two rectangular primes rather than one square prime) make detailed cross-study comparisons unwarranted. As 60-Hz flicker is within the established limits of the gamma band and is generally not detectable by observers in the present paradigm, in the following experiments we used 60-Hz primes.

Experiment 2

In Experiment 2 we used a go/no-go discrimination paradigm to assess the impact of asynchronous and synchronous primes on processing of a spatial relation between two ambiguous objects. In particular, observers were to press a key if the Kanizsa-type rectangles had different orientations and were to withhold a response otherwise. The go/no-go task tends to produce less variable responses than does the corresponding same/different task and therefore is often preferred in studies of object recognition (Biederman & Gerhardstein, 1993; Tarr, Williams, Hayward, & Gauthier, 1998). The "go-on-different" procedure avoids a potential alternative decision strategy that observers might use if they were asked to make explicit "same" responses.[1]

Method

Participants. Thirty-three UCLA students participated in Experiment 2. Seventeen participants, each paid $10 to participate in a 30-min session, were graduate students and undergraduate research assistants in cognitive psychology. The other 16 participants were UCLA undergraduates enrolled in the psychology department participant pool and received course credit.

Materials. The prime frames were identical to those used in the detection task in Experiment 1. On each trial, four frames were cycled at 60 Hz for 1.2 s. An additional final random frame was displayed for 17 ms to end the prime sequence, so that the initial and final frames were random in all conditions. After a 37-ms interstimulus interval (ISI), a target appeared, and observers decided whether the Kanizsa-type rectangles were oriented in the same or different directions. A 37-ms ISI is in the range found to be maximally effective by Elliott and Müller (2000).

Junction elements in the target display subtended 15′ of visual angle and were separated horizontally and vertically by 1°10′ of visual angle. Each junction element was composed of one or two lines. The width of junction lines was 3′ of visual angle. The target display consisted of 36 junction elements (six horizontal lines, six vertical lines, and six right angles in each of four different orientations). The locations of the two target rectangles were constrained such that no rectangle included the center fixation dot inside, the two rectangles did not intersect at any prime location, and they were never aligned horizontally or vertically. Otherwise, locations of the two rectangles were randomized for each set of frames, yielding a total of 12 possible rectangle pairs for each Prime × Response Type combination. A red dot (30′ of visual angle in diameter) was continually shown at the center of the screen, and observers were instructed to fixate on it throughout the trial.

Design and procedure. The experiment consisted of 480 trials with 60-Hz primes, of which 160 were asynchronous, 160 were synchronous, and 160 were random. For each prime type, the two rectangles in the target had the same orientation (equally often both vertical or both horizontal) on half the trials, and different orientations on the other half. Because of the nature of the go/no-go paradigm, we only collected data for *different* trials. We instructed observers to press a key (the right arrow with their right hand) if the two Kanizsa-type rectangles were oriented in different directions (one horizontal and another vertical), as quickly as possible with a 1-s deadline. They were to withhold a response if the rectangles had the same orientation. A beep sounded if the participant exceeded the deadline or made an error of commission or omission. The next trial started automatically 2 s after the previous target appeared.

All trial types were randomly intermixed. If the participant made an error on a trial, the computer emitted a beep. A target image was presented for 1 s and then disappeared from the display window. The next trial began automatically 0.5 s after the target image disappeared. The trials were presented in three blocks, with a 2-min rest period between each block. One or more practice blocks, each with 50 practice trials, preceded the test session. If the participant made errors on more than 10 trials in a block, we administered an additional practice block until the participant reached the accuracy criterion.

---

[1] The JIM model predicts that firing two separate rectangles in synchrony with one another will result in different patterns of activation on orientation-sensitive neurons as a function of whether the rectangles have the same or different orientations. Rectangles that have the same orientation will tend to strongly activate the neurons coding their shared orientation, whereas rectangles of differing orientations will tend to produce a diffuse pattern of activation over a wider array of orientation-sensitive neurons. Accordingly, synchronous primes on *same* trials will tend to produce sharply peaked activation over a small subset of orientation-sensitive neurons, whereas synchronous primes on *different* trials will tend to result in a weaker, more spread-out pattern of activation over the orientation-sensitive neurons. Therefore, an observer might respond quickly after synchronous primes on the basis of especially strong activation of orientation-specific neurons when rectangles share the same orientation. In preliminary studies, we found that synchronous (as well as asynchronous) primes indeed yielded reliable facilitation for *same* judgments (but not for *different* judgments) in a two-alternative forced-choice same/different task; synchronous primes also facilitated responses in a go/no-go paradigm with "go on same." In Experiment 2 we used a go-on-different task to reduce the possibility that observers could exploit an alternative holistic decision strategy. For the same reason, in Experiment 3 all trials displayed two rectangles with different orientations.

Results and Discussion

We excluded data from 6 participants (2 paid, 4 unpaid) because their error rates on *same* trials exceeded 10%, indicating a strong bias to press the *go* key. We performed all analyses on data from the remaining 27 participants. The RT priming results (correct trials only) for 60-Hz go-on-different trials are presented in Figure 3 for each prime condition. Geometric means of RTs were used because they are less susceptible to outliers (Alf & Grossberg, 1979; arithmetic means yield the same rank order of conditions). A within-subject analysis of variance revealed a significant main effect of prime condition, $F(2, 52) = 5.57$, $p < .01$, with mean RTs of 809, 819, and 823 ms for the asynchronous, synchronous, and random primes, respectively. Planned contrasts indicated that, relative to the random baseline, the asynchronous primes yielded 14-ms facilitation, $F(1, 26) = 15.13$, $p < .01$, whereas the synchronous primes yielded an unreliable 4-ms facilitation, $F(1, 26) = 0.59$, $p = .45$. A third planned comparison revealed that the asynchronous primes resulted in reliably greater facilitation than did synchronous primes, $F(1, 26) = 5.75$, $p = .02$. Error rates for the asynchronous, synchronous, and random prime conditions were 4% in each condition.

The results of Experiment 2 reveal that asynchronous primes facilitated identification of rectangles that differed in orientation, whereas synchronous primes yielded reliably less facilitation than did asynchronous primes and did not differ significantly from the random-prime baseline condition. These findings suggest that asynchronous primes facilitate perception of separate rectangles as separate objects with their own properties (in this case, orientations), as is predicted by the JIM model.

Experiment 3

The JIM model predicts that temporal structure is critical for visual binding whenever a task requires the individuation of multiple objects in a display. This requirement is expected to arise whenever observers must make a relational judgment about two objects (with the assumption that no holistic strategy is available; see Footnote 1). We designed Experiment 3 to increase the generality of our findings by examining the impact of gamma-band priming in a new discrimination task. Instead of judging whether two Kanizsa-type rectangles had the same or different orientations, observers in Experiment 3 were required to judge whether two rectangles were arrayed in an above/below relation or in a beside relation (see Figure 4).

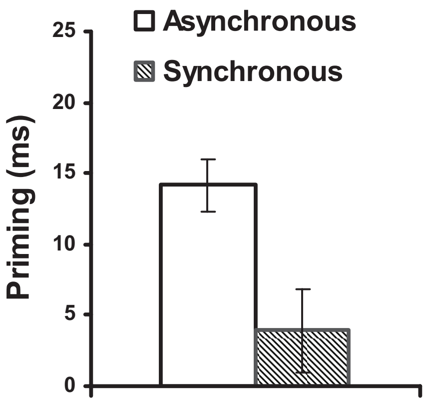

Figure 3. Priming of geometric mean correct reaction times (plus or minus standard error of measurement) for Experiment 2 ("go-on-different" responses).

The JIM model predicts that such relative-location judgments, like the same/different discrimination examined in Experiment 2, will be facilitated by asynchronous priming. Synchronous priming, by contrast, should not be as effective in facilitating the perception of rectangles as separate objects.

Method

Participants. Twenty-six UCLA undergraduates enrolled in the psychology department participant pool participated to receive course credit.

Materials, design, and procedure. The materials were identical to those used in the 60-Hz trials of Experiment 2, except that all target displays contained two rectangles of different orientations (one vertical and one horizontal). The experiment consisted of 480 trials with 60-Hz primes, of which 160 were asynchronous, 160 were synchronous, and 160 were random. The observers' task was to judge the relative spatial position of the two rectangles. For each prime type, the two rectangles in the target were arranged vertically on half the trials and horizontally on the other half (see Figure 4). The trial types were further subdivided equally into those in which the two Kanizsa-type rectangles were adjacent and those in which the rectangles were separated by one row or column of the 6 × 6 array. Observers pressed one of two keys (the right arrow with their right hand for *above/below*, and the control key with their left hand for *beside*).

All trial types were randomly intermixed. If the participant made an error on a trial, the computer made a beep. The next trial began automatically 1 s after a response was made. The total of 480 trials were presented in three blocks, with a 2-min rest period between each block. Fifty practice trials preceded the test trials.

Results and Discussion

We excluded from the analyses data from 2 participants who were exceptionally slow in their responses (mean RTs over 1,000 ms). The RT priming results (correct trials only) for the remaining 24 participants are presented in Figure 5 for each prime condition. Means are geometric (arithmetic means yield the same rank order of conditions). A within-subject analysis of variance with factors of prime type (asynchronous, synchronous, or random), relative location (above/below or beside), and spacing between Kanizsa-type rectangles (adjacent or separated) revealed a main effect of prime condition, $F(2, 46) = 3.47$, $p = .04$, with mean RTs of 664, 672, and 673 ms for asynchronous, synchronous, and random primes, respectively. Planned orthogonal contrasts indicated that the asynchronous condition yielded reliable facilitation relative to the synchronous and random conditions combined, $F(1, 23) = 7.46$, $p = .01$; the latter conditions did not differ, $F(1, 23) = 0.09$, $p = .77$. A separate (nonorthogonal) test directly comparing the amount of priming produced by asynchronous versus synchronous primes fell just short of significance, $F(1, 23) = 3.81$, $p = .06$. No other main effects or interactions were reliable. Error rates for the asynchronous, synchronous, and random prime conditions were very low and identical across conditions (2%).

The results of Experiment 3 serve to increase the generality of our findings. In particular, 60-Hz asynchronous primes, which the JIM model predicts will facilitate the perception of rectangles as separate objects, proved to be effective in reducing RTs to discriminate whether two Kanizsa-type rectangles were arranged above and below one another or beside one another in a display. In contrast, synchronous primes were ineffective in this task.

General Discussion

The present study extends the priming paradigm introduced by Elliott and Müller (1998, 2000, 2001) to relational judgments based on multiobject displays. The results demonstrate that visual information presented as temporally structured flicker in the gamma band can modulate judgments about the spatial relation between objects. Experiment 1 demonstrates that observers were unable to detect temporal structure in primes presented at the rate of 60 Hz. Experiment 2 demonstrates facilitation for same/different discriminations, using a go/no-go paradigm with "go on different," when an asynchronous prime was presented at 60 Hz prior to the two static rectangles on which the decision was based. Experiment 3 demonstrates analogous facilitation for above/below versus beside judgments. The finding of priming by asynchronous flicker is consistent with the JIM model of visual binding (Hummel, 2001; Hummel & Biederman, 1992; Hummel & Stankiewicz, 1996), according to which multiple objects or parts are represented by synchronized firing of neurons for the features of each individual object or part, with neurons representing the features of separate objects or parts firing out of synchrony with one another. In contrast, we did not obtain reliable priming by synchrony either in the same/different discrimination (5-ms difference from baseline in Experiment 2) or for above/below versus beside judgments (1-ms difference from baseline in Experiment 3). For both types of judgments, priming by asynchrony thus proved to be more effective than priming by synchrony.

The weaker priming observed for synchronous than for asynchronous flicker is counterintuitive, as the synchronous primes were more similar to the subsequent target displays, in which two static rectangles appeared together. However, the JIM model (Hummel & Biederman, 1992; Hummel & Stankiewicz, 1996) can provide a framework for understanding the results observed with synchronous primes. In contrast to asynchronous primes, synchronous primes should not only bind the features of the individual rectangles but also bind the two rectangles into a single, unified percept. To the extent that the same versus different orientation and above/below versus beside judgments required observers to perceive the rectangles as distinct objects, synchronizing them could interfere with the comparison.

Overall, our findings clearly establish that priming by asynchrony can facilitate relational judgments based on multiobject displays. These findings add support to the hypothesis that phase locking in the gamma band is a neural solution to the binding problem in human visual perception and, in particular, in the binding of objects or parts to their spatial relations. (See Krishnan, Skosnik, Vohs, Busey, & O'Donnell, 2005, for recent work relating gamma-band activity to perception of coherent motion.) Our findings are generally consistent with those of Elliott and Müller (1998, 2000, 2001), who found that synchronous flicker primed detection of single objects. There are some parametric differences in the present extension to relational judgments with multiobject displays. In particular, Elliott and Müller (1998) found that 40-Hz flicker yielded optimal facilitation without being detectable by observers, whereas we observed similar phenomena using more rapid 60-Hz flicker. It is possible that the neural representation of relations among objects makes use of a higher frequency portion of the gamma band than does the neural representation of features of a single object. However, as we noted in the *Results and Discussion* section of Experiment 1, numerous procedural differences between our displays and those used by Elliott and Müller make it premature to draw any strong conclusions about possible neural differences between single-object and multiobject binding. It is desirable to compare judgments involving different types of binding with closely matched stimuli and displays.

Figure 4. Target displays used in Experiment 3 for judgments of *above/below* versus *beside*. A: rectangles arranged vertically (and adjacent); B: rectangles arranged horizontally (and separated).

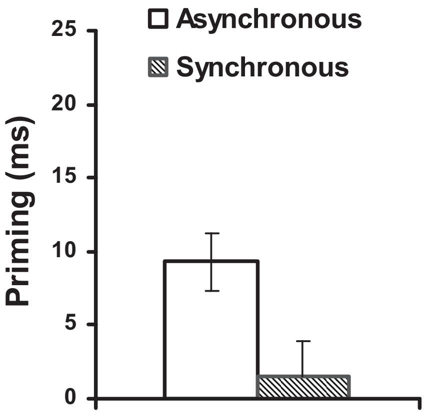

Figure 5. Priming of geometric mean correct reaction times (plus or minus standard error of measurement) for Experiment 3 (judgments of *above/below* vs. *beside*).

The binding problem in visual perception is a special case of the more general problem of how the brain codes elements and relations, maintaining both the identities of the elements and the nature of the relations among them. Binding elements into relations is also fundamental to human language and reasoning. In addition to providing a neural basis for binding in visual perception, it is possible that temporal structure is fundamental to more abstract cognitive processes (Hummel & Holyoak, 1992, 1997, 2003; Ihara et al., 2003). If so, this common mechanism suggests an important link between the neural bases of perception and of abstract thought.

References

Alf, E. F., & Grossberg, J. M. (1979). The geometric mean: Confidence limits and significance tests. *Perception & Psychophysics, 26,* 419–421.

Biederman, I. (1987). Recognition by components: A theory of human image understanding. *Psychological Review, 94,* 115–147.

Biederman, I., & Gerhardstein, P. C. (1993). Recognizing depth-rotated objects: Evidence and conditions for three-dimensional viewpoint invariance. *Journal of Experimental Psychology: Human Perception and Performance, 19,* 1162–1182.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Busey, T. A., & Loftus, G. R. (1994). Sensory and cognitive components of visual information processing. *Psychological Review, 101,* 446–469.

Csibra, G., Davis, G., Spratling, M. W., & Johnson, M. H. (2000, November 24). Gamma oscillations and object processing in the infant brain. *Science, 290,* 1582–1585.

Dorfman, D. D., & Alf, E. (1969). Maximum-likelihood estimation of parameters of signal-detection theory and determination of confidence intervals—Rating-method data. *Journal of Mathematical Psychology, 6,* 487–496.

Eckhorn, R., Bauer, R., Jordan, W., Brish, M., Kruse, W. Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: A mechanism of feature linking in the visual cortex? Multiple electrode and correlation analysis in the cat. *Biological Cybernetics, 60,* 121–130.

Elliott, M. A., Herrmann, C. S., Mecklinger, A., & Müller, H. J. (2000). The loci of oscillatory visual-object priming: A combined electroencephalographic and reaction-time study. *International Journal of Psychophysiology, 38,* 225–241.

Elliott, M. A., & Müller, H. J. (1998). Synchronous information presented in 4-Hz flicker enhances visual feature binding. *Psychological Science, 9,* 277–283.

Elliott, M. A., & Müller, H. J. (2000). Evidence for 40-Hz oscillatory short-term visual memory revealed by human reaction-time measurements. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 703–718.

Elliott, M. A., & Müller, H. J. (2001). Effects of synchrony on mechanisms of perceptual organization. *Visual Cognition, 8,* 655–677.

Green, C. B., & Hummel, J. E. (2004). Relational perception and cognition: Implications for cognitive architecture and the perceptual-cognitive interface. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 44, pp. 201–223). San Diego, CA: Academic Press.

Haig, A. R., Gordon, E., Wright, J. J., Meares, R. A., & Bahramali, H. (2000). Synchronous cortical gamma-band activity in task-relevant cognition. *NeuroReport, 11,* 669–675.

Hummel, J. E. (1999). Binding problem. In R. A. Wilson & F. C. Keil (Eds.), *The MIT encyclopedia of the cognitive sciences* (pp. 85–86). Cambridge, MA: MIT Press.

Hummel, J. E. (2001). Complementary solutions to the binding problem in vision: Implications for shape perception and object recognition. *Visual Cognition, 8,* 489–517.

Hummel, J. E., & Biederman, I. (1992). Dynamic binding in a neural network for shape recognition. *Psychological Review, 99,* 480–517.

Hummel, J. E., & Holyoak, K. J. (1992). Indirect analogical mapping. In *Proceedings of the fourteenth annual conference of the Cognitive Science Society* (pp. 516–521). Hillsdale, NJ: Erlbaum.

Hummel, J. E., & Holyoak, K. J. (1997). Distributed representations of structure: A theory of analogical access and mapping. *Psychological Review, 104,* 427–466.

Hummel, J. E., & Holyoak, K. J. (2003). A symbolic-connectionist theory of relational inference and generalization. *Psychological Review, 110,* 220–264.

Hummel, J. E., & Stankiewicz, B. J. (1996). An architecture for rapid, hierarchical structural description. In T. Inui & J. McClelland (Eds.), *Attention and performance XVI: Information integration in perception and communication* (pp. 93–121). Cambridge, MA: MIT Press.

Hummel, J. E., & Stankiewicz, B. J. (1998). Two roles for attention in shape perception: A structural description model of visual scrutiny. *Visual Cognition, 5,* 49–79.

Ihara, A., Hirata, M., Sakihara, K., Izumi, H., Takahashi, Y., Kono, K., et al. (2003). Gamma-band desynchronization in language areas reflects syntactic process of words. *Neuroscience Letters, 339,* 135–138.

Keele, S. W., Cohen, A., Ivry, R., Liotti, M., & Yee, P. (1988). Test of a temporal theory of attentional binding. *Journal of Experimental Psychology: Human Perception and Performance, 14,* 444–452.

König, P., & Engel, A. K. (1995). Correlated firing in sensory-motor systems. *Current Opinion in Neurobiology, 5,* 511–519.

Krishnan, G. P., Skosnik, P. D., Vohs, J. L., Busey, T. A., & O'Donnell, B. F. (2005). Relationship between steady-state and induced gamma activity to motion. *NeuroReport, 16,* 625–630.

Lee, K. H., Williams, L. M., Breakspear, M., & Gordon, E. (2003). Synchronous gamma activity: A review and contribution to an integrative neuroscience model of schizophrenia. *Brain Research Review, 41,* 57–78.

Lee, S.-H., & Blake, R. (1999, May 14). Visual form created solely from temporal structure. *Science, 284,* 1165–1167.

Lisman, J. (1998, July 9). Neuroscience: What makes the brain's tickers tock. *Nature, 394,* 132–133.

Luck, S. J., & Vogel, E. K. (1997, November 20). The capacity of visual working memory for features and conjunctions. *Nature, 390,* 279–281.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442.

Rodriguez, E., George, N., Lachaux, J. P., Martinerie, J., Renault, B., & Varela, F. J. (1999, February 4). Perception's shadow: Long-distance synchronization of human brain activity. *Nature, 397,* 430–433.

Shipley, T. F., & Kellman, P. J. (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Perception & Psychophysics, 52,* 97–106.

Singer, W. (2004). Synchrony, oscillations and relational codes. In L. M. Chalupa & J. S. Werner (Eds.), *The visual neurosciences* (2nd ed., pp. 1665–1681). Cambridge, MA: MIT Press.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18,* 555–586.

Stankiewicz, B. J., & Hummel, J. E. (2002). The role of attention in scale- and translation-invariant object recognition. *Visual Cognition, 9,* 719–739.

Stankiewicz, B. J., Hummel, J. E., & Cooper, E. E. (1998). The role of attention in priming for left–right reflections of object images: Evidence for a dual representation of object shape. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 732–744.

Tarr, M. J., Williams, P., Hayward, W. G., & Gauthier, I. (1998). Three-dimensional object recognition is viewpoint dependent. *Nature Neuroscience, 1,* 275–277.

Thoma, V., Hummel, J. E., & Davidoff, J. (2004). Evidence for holistic representations of ignored images and analytic representations of attended images. *Journal of Experimental Psychology: Human Perception and Performance, 30,* 257–267.

Usher, M., & Donnelly, N. (1998, July 9). Visual synchrony affects binding and segmentation processes in perception. *Nature, 394,* 179–182.

von der Malsburg, C. (1994). The correlation theory of brain function. In E. Domany, J. L. van Hemmen, & K. Schulten (Eds.), *Models of neural networks II* (pp. 95–119). Berlin: Springer.

von der Malsburg, C. (1995). Binding in models of perception and brain function. *Current Opinion in Neurobiology, 5,* 520–526.

Received March 29, 2005
Revision received October 17, 2005
Accepted October 22, 2005 ■