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Abstract

How does neuronal activity bring about the interpretation of visual space in terms of objects or complex perceptual events? If they group, simple visual features can bring about the integration of spikes from neurons responding to different features to within a few milliseconds. Considered as a potential solution to the "binding problem," it is suggested that neuronal synchronization is the glue for binding together different features of the same object. This idea receives some support from correlated- and periodic-stimulus motion paradigms, both of which suggest that the segregation of a figure from ground is a direct result of the temporal correlation of visual signals. One could say that perception of a highly correlated visual structure permits space to be bound in time. However, on closer analysis, the concept of perceptual synchrony is insufficient to explain the conditions under which events will be seen as simultaneous. Instead, the grouping effects ascribed to perceptual synchrony are better explained in terms of the intervals of time over which stimulus events integrate and seem to occur simultaneously. This point is supported by the equivalence of some of these measures with well-established estimates of the perceptual moment. However, it is time in extension and not the instantaneous that may best describe how seemingly simultaneous features group. This means that studies of perceptual synchrony are insufficient to address the binding problem.

Our ability to extract structure from the mosaic of ambient visual information raises an as yet unresolved question for perceptual neuroscience. Known as the "binding problem," this question asks how neuronal activity can bring about the organization of visual space into definable subregions resolvable as objects or as complex perceptual events. Physiological studies have shown that simple visual features can bring about the temporal alignment of spikes from a number of neurons to within a few milliseconds of one another, if those features group. A number of psychophysical paradigms have attempted to corroborate the physiological binding hypothesis and seem to have enjoyed some success: The first of these approaches involves "periodic motion" or the alternate presentation of sets of display elements in different phases of a global presentation frequency (Kandil & Fahle, 2001; Leonards, Singer, & Fahle, 1996; Fahle, 1995). Using this technique, it has been shown that the global orientation of elements in a target presentation frame may be judged with greater than chance probability as a function of the onset asynchrony between the target and a second frame containing background elements. A second technique, referred to in terms of "stochastic" (or "correlated") motion, involves presentation of a field of Gabor patches which individually and seemingly at random reverse in phase, thereby effecting a form of apparent motion similar to that of a running machine. The critical modification in this paradigm involves the temporal correlation of phase reversals, which can bring about perception of a figural region consisting of those elements which change phase at the same time (Lee & Blake, 1999; Alais, Blake, & Lee, 1998).

At first glance, the use of periodic and correlated motion appears to support the idea that synchrony can bring about the organization of visual space: On the one hand, a figural region emerges with the desynchronization of figural elements from their background, whereas figural regions appear to emerge solely as a function of the correlated motion of their elements. In fact, in the case of periodic motion, a direct link between psychophysical binding and physiological timing seems particularly promising when it is considered that a figural region emerges when the onset of figure and ground are desynchronized by intervals of as little as 7 msec (Fahle, 1995). By a reversal of logic, this permits temporal integration to operate within windows close to a limit of around 10 msec, which is around the maximum separation in time between synchronized spikes. In the case of correlated motion, perception of a figural region seems to come about as a result of perfectly correlated phase reversals. Both lines of evidence lay very strong emphasis on the idea that the segmentation or emergence of figural subregions comes about as a function of the temporal synchrony/asynchrony of figure and ground. In fact, this outcome has been explicitly equated with the temporal synchronization of neurons responding to the presence of simple visual features that group (Alais et al., 1998). Nevertheless, and in spite of these claims, figure-ground
separation akin to that demonstrated by Lee and Blake (1999) has been shown to arise by virtue of temporal bandpass filtering. A physiologically plausible temporal bandpass filter has been shown to convert the different pattern in phase reversals between figure and background elements into a classic spatio-temporal contrast cue. This can signal the figural subregion irrespective to the synchrony or otherwise of the motion reversals (Adelson & Farid, 1999) and clearly questions the “necessity” of a mechanism sensitive to temporal synchrony (Farid, 2002).

Our concern in this article is connected with a problem of induction, so fundamental that it obliges rejection of perceived synchrony as “sufficient,” an explanation for the effects of either correlated or periodic motion. The problem is founded on the fairly common observation that events may be perceived as synchronous (or simultaneous) beyond the case where the two events occur at precisely the same time. In fact, and depending upon stimulus conditions, perceptual simultaneity may be experienced between stimulus events separated by intervals of between zero milliseconds (true simultaneity) to a few tens, if not over a hundred milliseconds, while there may be little or no difference between perceptions of synchrony following presentation of physically simultaneous events and perceptions that follow presentation of nonsimultaneous events. So why is this problematic for perceptual synchrony? The synchrony or “simultaneity problem” proper arises when we ask the question “to what extent can we claim to have experienced events as simultaneous?” At the crux of the problem are events that are nonsimultaneous but which we see as simultaneous and it might be considered an acceptable claim that, irrespective of the actual simultaneity of two events, in perception events can be considered simultaneous if that is how they seem to the observer (Kelly, 2005). However, the following logic modifies this consideration.

Take any two events \( A_1 \) and \( A_2 \) that appear to the observer to occur simultaneously, despite being separated by some interval. Take then some third event that occurs at some time later than both \( A_1 \) and \( A_2 \) but is experienced as simultaneous with each. Using this method, a series of events from sets \( \{A_1, A_n\} \) may be experienced as simultaneous although the point may be reached at which \( A_1 \) and \( A_n \) come to be experienced as nonsimultaneous. Perceived simultaneity is thus nontransitive (i.e., \( A_1 = A_2 \) and \( A_2 = A_n \) but \( A_1 \neq A_n \)) and nontransitivity should, in principle, preclude a definition that includes simultaneity because simultaneity cannot be both nontransitive and an equivalence relation. It seems an obvious solution to circumvent the problem of transitivity two events may be defined as perceptually simultaneous if (and only if) they appear to be simultaneous and if (and only if) there is no third event with which one event appears to be simultaneous while the other does not. Indeed, this counterargument might be valid if it were not for the following corollary: Although two events might appear to be simultaneous, it is nonetheless impossible for the observer to conclude that they have experienced them to be simultaneous without reference to the third, nonsimultaneous event. This event thus marks both the limit of perceived simultaneity and indeed the maximum interval of time between which the two key events would have been perceived as simultaneous. On these grounds, perceptual synchrony seems little more than a non sequitur which lacks construct validity unless taken to refer to the interval of time over which two or more events are seen to occur at the same time.

It is clear that this conclusion requires development, especially when it is considered that simultaneity thresholds can vary quite widely from between 3 and 5 msec to more than 100 msec and are known to depend upon stimulus conditions (Elliott, Shi, & Sürer, in press; von Békésy, 1936; Exner, 1875). A review of the evidence brings to light an upper threshold for temporal integration, which has been estimated on a number of occasions to be at around 55 msec. This interval seems promising in that it represents the minimal time required for the perceptual separability of two or more events presented repeatedly and in sequence (Elliott et al., in press; Brecher, 1932). It also seems pertinent to periodic motion stimuli, which are repeatedly presented in sequences, and it may also refer to correlated motion because, as demonstrations show, more than one phase reversal is required to perceive the correlated subregion. On these assumptions, it seems reasonable to assume 55 msec as a candidate threshold below which repeating events, simultaneous or otherwise, will be experienced as occurring at the same time, whereas for separations of greater than 55 msec, events will be seen as successive, and thus, asynchronous.

Although promising, on the basis of existing data, a thorough evaluation of this idea in the context of either periodic or correlated motion is limited: Because they emphasize the effect of perfect correlation, the correlated motion paradigm is uninformative with respect to the upper limit in time, expressed in terms of the cross correlation of motion reversals, beyond which the figural subregion is no longer perceived. This is not quite the case for periodic motion. In this case, measures do exist that are consistent with the idea that for presentations falling within a given window of time all stimuli that appear together will be bound together, whereas stimuli falling outside of these intervals will tend to be seen as separate. In fact originally, the emergence of figural subregions was described in terms of the necessary temporal delays between rapidly alternating stimulus frames. Interestingly, for spatially stochastic (random point) patterns, delays were relatively constant over a range of lower frequencies 1.3—around 15–20 Hz, at which point the required delays were found to decrease in magnitude (Fahle, 1993). Although the reasons for this decrease are not known, it seems reasonable to speculate that the
psychophysical simultaneity threshold may represent a dividing line between one set of process dynamics, which at optimal tuning permit perception of an asynchrony, and a second set which, although optimized, still cannot resolve two stimuli as separated in time. Evidence suggesting an interval of 50 to around 60 msec as significant can be inferred from other work employing alternating or repeating stimulus presentation (see e.g., Elliott et al., in press; Holcombe & Cavanagh, 2001; Kandil & Fahle, 2001; Bartels & Zeki, 1998; Moutoussis & Zeki, 1997). For example, Elliott and colleagues found simultaneity thresholds to be at around 60 msec for two illuminated bars that separately and repeatedly increase in luminance. Spatially superimposed pairings of alternating orientation and color features are perceptually separable when presented at frame-by-frame separations of, on average, 55 msec and higher (Holcombe & Cavanagh, 2001). Kandil and Fahle (2001) have shown that the interaction of form and temporal cues requires no less than 50–60 msec for a figural region to be seen, whereas different attributes of a visual scene, such as the color and the direction of motion or the color and the orientation of lines, may be misbound (Bartels & Zeki, 1998) with color perceived before orientation by 63 msec, orientation 52 msec before motion, and color 118 msec before motion (i.e., 2 * 59 msec) (Moutoussis & Zeki, 1997).

In conclusion, our argument states that perceptual synchrony is not sufficient to describe the perceptual effects arising visual events that take place in very close temporal proximity. An alternative explanation is that the effects of periodic and correlated motion are a function of the interval of time over which two or more events are perceived to be in synchrony. On these grounds, there is no basis for considering any current measures of perceptual synchrony as support for the common claim that neuronal synchrony is a means for the binding of perceptual features. But this is not to say that the information that appears to go together when presented within a given interval of time is not bound together, it is just to say that it cannot be claimed to be bound merely by virtue of its simultaneous appearance. Instead, and as a potential factor for inclusion into the calculus that links mind and brain, it seems more promising to include the simultaneity threshold itself as a more parsimonious (and seemingly replicable) measure of when two or more events appear to the observer as if they occur in synchrony. This is because several different paradigms agree with classical estimates in showing stimuli presented in sequence to be seen as a simultaneity when separated by intervals of less than around 53–60 msec. What remains to be investigated is the generalizability of this value to both periodic and correlated motion and what also remains to be examined is the extent of integration windows for stimuli that are synchronized but are not presented in sequences. Nevertheless, the most important first step seems to be deciding the neural correlates of simultaneity perception and, in this context, examining which stimulus characteristics decide the interval at which the simultaneity threshold is located. This is especially the case given the extent to which they may vary even within a single experimental paradigm (see e.g., Fahle, 1993). Following research agenda of this nature holds some considerable promise for the uncovering the temporal characteristics in psychophysical performance that are analogous to the temporal characteristics of neural activity.

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REFERENCES