

CHAPTER 23

DYNAMIC ATTENTION

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INTRODUCTION: TRACKING EVENTS AS THEY UNFOLD IN TIME

IN order to process the events around us we must select and keep track of the objects of current interest, ignoring others around them. This indexing or individuation of targets is a central function of attention and here we will examine how it operates during dynamic events, some as simple as a moving dot, others as complex as moving human forms. This indexing of targets maintains the continuity of their identity as they change and move. This requirement of continuity was defined by Ternus (1926, 1938) as ‘the problem of phenomenal identity’ and since then there have been several proposals to fill this role: object files (Kahneman, Treisman, and Gibbs 1992), Fingers of Instantiation or FINSTs (Pylyshyn 1989, 2000, 2001), deictic codes (Ballard, Hayhoe, Pook, and Rao 1997), and attention pointers (Cavanagh, Hunt, Afraz, and Rolfs 2010). These concepts are closely related, all providing temporary representations of the objects of interest—representations that index or point to the properties of the object, such as its features, history, location, and identity. This is of critical importance if the target is moving, as we can no longer interrogate its properties by accessing the same location in space. We must know where it has gone. In this chapter, we trace the evidence that these temporary representations are the functional core of attention: they control the selection of input and they have limited capacity. We will review six key properties of dynamic attention: (1) its ‘identity’ operation that individuates moving, changing targets; (2) the role of the motion trajectory; (3) spatiotemporal limits; (4) anatomical locus; (5) temporal structure; and (6) temporal salience maps. Two differences emerge that distinguish dynamic attention from standard spatial attention: first, temporal limits on selection become spatiotemporal limits, extending over space and time; and second, the controlling anatomical structures show bilateral rather than contralateral properties.

TRACKING TARGETS: IS IT ATTENTION OR IS IT LOW-LEVEL MOTION?

Dynamic attention keeps the location of selection focused on the target of interest as it moves. In doing so, it fills the fundamental role of keeping track of the target, maintaining the continuity of the target's identity as it moves. This tracking operation has been most widely studied in the multiple-object tracking task (Pylyshyn and Storm 1988; see review, Cavanagh and Alvarez 2005). In these experiments, several items are moving independently, a few of which are the targets. These targets are distinguished from the distractors only by their history—they began life in the display highlighted with a different colour or with flicker. Once this marking is extinguished, however, they are identical to the non-targets in the display, and differentiated only in the subject's mind. The task is of course a spatial as well as temporal one and if the items are too close together, the tracking fails for reasons of crowding—the identity of the targets and distractors cannot be kept independent if the targets cannot be individuated. But it is in the pure sense spatiotemporal. When the speed of items increases, the ability to keep track is reduced (Alvarez and Franconeri 2007; Holcombe and Chen 2012) even though the spacing is not changed.

Tracking multiple objects with attention certainly feels effortful. However, on its own, that is not actual evidence that the tracking is an attentional process. Nevertheless, recent results (e.g. Drew, McCollough, Horowitz, and Vogel, 2010) now strongly favour the direct role of attention in tracking. These results overturned the earlier findings that surprisingly did not show any evidence of the role of attention for tracking the targets. In particular, Pylyshyn and Annan (2006) presented test probes either on the tracked targets, on the distractors, or in empty space to see if there was a performance advantage for probe detection on the tracked targets. These results showed a deficit for probes on the distractors but no advantages and no differences for probes in empty space or on the tracked targets. However, Drew et al. (2010) argued that the dual task nature of this experiment disrupted normal allocation of attention. Specifically, having to detect probes on the distractors and in empty space forced subjects to unnaturally allocate attention away from the targets. To address this, they used event-related potential (ERP) measures of response to brief probes that the subjects were told to ignore. In this case, attentional enhancement of the ERP response was seen strongly on the tracked targets, weakly on the distractors, and most weakly in empty space (and on static distractors). These results provided direct evidence for what seems obvious to anyone who tries the multiple object-tracking task: spatial attention is strongly allocated to each target.

Brain imaging as well as transcranial magnetic stimulation (TMS) experiments also show the involvement of attentional areas during the multiple object-tracking task (Culham, Brandt, Cavanagh et al. 1998; Culham, Cavanagh, and Kanwisher 2001; Howe, Horowitz, Morocz et al. 2009; Jovicich, Peters, Koch et al. 2001; Shim, Alvarez, Vickery, and Jiang 2010; Battelli, Alvarez, Carlson, and Pascual-Leone 2009). More specifically,

certain areas in frontal and parietal cortex modulate their activity as a function of the number of items being tracked. Roelfsema, Lamme, and Spekreijse (1998) have shown in a related curve-tracing task that enhanced neural activity can be detected moving along the path over which attention would be expected to move during the task. Overall, the behavioural, electrophysiological, and neurophysiological evidence all support the hypothesis that tracking is accomplished by maintaining a focus of attention over each target as it moves (attention pointers, Cavanagh et al. 2010). These results argue against Pylyshyn's original claims (1989) that the targets are indexed by non-attentional processes.

While attention is clearly involved in tracking, there is something special about the motion of the targets that helps keep attention locked on to its position. For example, Horowitz, Holcombe, Wolfe et al. (2004) asked subjects to move their attention across a set of targets arranged in a circle around fixation. They found that the subjects could shift attention much more rapidly if the targets appeared to be jumping than if they were static and attention had to switch from one to the next. Hogendoorn, Carlson, and Verstraten (2007) made essentially the same point in a similar experiment. This suggests that the motion of the targets is critical in engaging a much more nimble, mobile attention, one that stays with a single target as it moves, rather than slowly disengaging from one and re-engaging with the next as it steps through a series of separate targets.

If motion is the key, however, it comes in two varieties: low-level and high-level (Anstis 1980; Braddick 1974; Julesz 1971; Cavanagh 1992; Lu and Sperling 1995). The low-level motion signals are provided by directionally tuned neurons in early visual areas. These units are activated when there is motion in their preferred direction within their small area of surveillance, their 'receptive field'. Low-level units respond to energy in the input without having to identify or categorize anything. They also respond whether or not attention is directed to the moving stimulus, although attention can produce improvements in response (e.g. 20% in area MT; Treue and Maunsell, 1996). The second variety is called high-level motion but some have argued that is really just another name for attentive tracking (Verstraten, Cavanagh, and Labianca 2000; Wertheimer 1912). It makes little sense to ask whether high-level motion (attentive tracking) is critical for attentive tracking but we can ask whether this high-level motion system just collates low-level signals and attributes them to the target object; or whether it solves the tracking problem on its own.

Continuously moving targets will certainly activate low-level motion mechanisms. Do these responses help to keep attention focused (Cavanagh et al. 2010) on the target? In fact, it is easy to show that low-level mechanisms are of little or no use in tracking objects. The first evidence that the tracking process is independent of low-level mechanisms is that subjects can track stimuli that do not drive low-level motion responses (St. Clair, Huff, and Seiffert 2010). However, there is a second and more fundamental argument against the contribution of low-level signals. Specifically, low-level motion is a local measurement based in retinal coordinates, not an object property. In order to use low-level motion signals, the object in question has to be segmented from the background in order to pick up only the object's signals independently of background

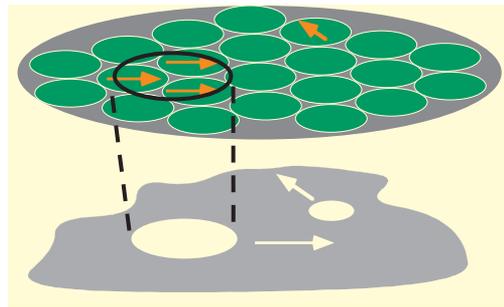


FIGURE 23.1 Low-level motion problematic for tracking targets. The visual system has to know where an object is to read out its low-level motion signals and avoid mixing them with other motions. This segmentation requires knowing where the object is at each moment. But if the object location is known on a moment-by-moment basis, there is no need to read out low-level motion. The object tracking problem is already solved.

motion. The segmentation therefore requires moment-to-moment knowledge of the object's location, in effect, requiring that the successful tracking of the object occur before the appropriate low-level signals can be encoded (see Fig. 23.1). Clearly, low-level motion cannot be of much help with tracking if tracking is a prerequisite for the help.

Fine, but could the low-level signal, once analysed from within the object's current boundaries, still help to determine the likely next location to find the target? Possibly, but clearly it is not essential (St. Clair et al. 2010), and often it is not possible because the recovery of global direction from low-level signals is frequently intractable (Rubin and Hochstein 1993). So it is not clear what the low-level signals could add, except perhaps, an after-the-fact sensation of the direction of the object's motion, in those cases where global motion extraction is possible. Here again, there is no need to extract motion from low-level signals, as the object's motion can be recovered from the attentive tracking signals. This is a process much like the one that recovers a target's motion when we track it with our eyes (smooth pursuit). In this case, when the pursuit is accurate, the target has little or no motion on the retina, and so little or no low-level motion signal. We nevertheless see it move. The signals that keep the eye on the target (efference copy) must provide the perception of motion for the target (e.g. Freeman and Banks 1998). Similarly, the signals that keep attention on a moving target, 'covert efference copy' (Cavanagh 1992), can provide a perception of motion for the target when the eyes are not moving. This is especially useful when the target does not activate low-level mechanisms (St. Clair et al. 2010). In this case, the objects are seen to slow or stop if they are not tracked, but when tracked they are perceived to move at close to their actual speed (Cavanagh 1992). In the study by St. Clair et al. (2010), the targets were patches of texture that had their own internal motion that could be consistent with the motion of the target itself or inconsistent. The internal motion was low-level, carried by local displacements of the luminance-defined texture, whereas the target's motion was high-level (not luminance defined). When the internal motion was inconsistent with the target's direction, tracking was impaired. This could suggest either that the low-level motion

signals were contributing to the tracking, perhaps helping to predict the next location for the target, or that the target's perceived locations were distorted by the low-level signals (Ramachandran and Anstis 1990) making it more difficult to keep track of target locations. The role of inconsistent low-level motion remains to be decided here, but the important point is that the absence of low-level motion does not impair tracking.

To summarize, stimuli that do not drive low-level motion mechanisms are nevertheless seen to move and can be tracked with attention. Moreover, the extraction of a target's motion (from displacement of an attention pointer that tracks it) is simpler than the extraction of global motion from low-level signals. In particular, the solution of target direction based on low-level motion requires an object segmentation that renders the low-level solution redundant, even if it were available.

Therefore, it would be more accurate to say that attentive tracking, high-level motion, is an independent system. This suggests that when contributions of low-level motion can be ruled out, research on high-level motion can be used to characterize the properties of dynamic attention, how it works, and how fast, and how far objects can be tracked as they move in continuous motion (multiple object-tracking tasks), or discrete jumps (apparent motion). We do not yet know how this tracking is accomplished but one outcome of the process is likely the updating of the target's activation, or attention pointer, on saccade maps (Cavanagh et al. 2010) to keep it locked on the target.

SPATIAL ATTENTION OPERATES ON OBJECTS; DYNAMIC ATTENTION OPERATES ON 'SPRITES'

Motion can tell us more than where an object is going; it can also tell us what the object is. The characteristic motions of familiar objects like a pencil bouncing on a table, a butterfly in flight, or a closing door can support the recognition of these objects. In return, once the object and its stereotypical motion are recognized, knowledge of that motion can support the continuing percept. Like the first notes of a familiar tune, our knowledge can guide our hearing of the remainder of the melody, filling in missing notes. Selfridge (1959) had argued that shape recognition was supported by legions of 'daemons' each of which detected whether a particular feature was present. We proposed dynamic versions of these agents, 'sprites' that would underlie the detection and representation of objects undergoing characteristic, stereotyped motions (Cavanagh, Labianca, and Thornton 2001). The suggestion is that dynamic attention does not operate on inert objects but on dynamic models that carry information not only about their identity and features but also about their expected motions. Point-light walkers make this point compellingly. A human form is easily recognized from the motions of a set of lights attached to a person filmed while walking in the dark (Johansson 1973; Neri, Morrone, and Burr 1998). Most importantly, Johansson (1973) proposed that the analysis relied specifically

on an automatic and spontaneous extraction of mathematically lawful spatiotemporal relations. However, this does not hold up. Search for point-light walkers is very inefficient, suggesting only one can be analysed at a time (Cavanagh et al. 2001). Perception of this compelling, characteristic motion requires attention and that is a key argument for bringing these processes under the umbrella of attention.

The central point of the sprite proposal is that dynamic attention must actively model the motions of targets rather than simply passively follow them. One hundred years ago, Max Wertheimer (1912) reported a percept of motion that could not be explained in terms of low-level motion. Using a tachistoscope, he presented a configuration of two intersecting lines and alternated this stimulus (a cross) with one that was rotated 45 degrees. In space-time, the lines of the cross have correlations of equal strength in both the clockwise and the counterclockwise direction. This results in an ambiguous percept where back and forth motion between the lines is often the initial impression. However, Wertheimer (1912) also noticed that this was not always true. In the case where ‘the lines stand normal to one another, and the distances are objectively equally favored, then it is *set and posture of attention* [. . .] that proved decisive in determining whether the rotation was seen towards the right or towards the left’ (our italics, translated in Shipley 1961: 1070).

This observation points out the importance of attentional mechanisms in perceiving motion under ambiguous stimulus conditions. Despite its early discovery, this phenomenon was not studied again until recently (e.g. Ramachandran and Anstis 1983; Cavanagh 1992; Verstraten et al. 2000).

These phenomena suggest that dynamic attention uses models of familiar or characteristic motions to track moving objects, whether the motion of a wheel or the stride of a person walking. We claim that the animations are played out by attentive processes in the same way that we can animate a mental image. With the object present in the visual field, the input image data act like set points in the progress of the animation, a technique often used in computer graphics. The advantage of the motion models is the same advantage that is offered by any recognition of a familiar pattern. Once enough of the pattern is acquired to recognize it, the rest can be filled in from memory. Sparse inputs can support rich percepts and in the case of a moving object, filling in implies a prediction of likely motions and tracking them with fewer data than would otherwise be necessary. These advantages have formed the basis of many theories of perception from schemata and schema theory (Bartlett 1932; Neisser 1967) to frames and scripts (Minsky 1975; Schank and Abelson 1977).

These results suggest that the visual system acquires and uses stored motion patterns, sprites, which are characteristic of familiar events or objects. We use these stored patterns to recognize and then animate our perception of familiar events. Our experience of these animation routines might suggest that they are effortless; however, our studies showed that they are not (Cavanagh et al. 2001; Battelli, Cavanagh, and Thornton 2003b).

The internal modelling of trajectories and speed can underlie the perception of simple motions as well as complex ones. A tracked object in smooth (Verstraten et al. 2000) or

random motion (Pylyshyn and Storm 1988) may be supported by the internal representation of its current and expected trajectory. We have proposed that high-level motion (cf. Anstis 1980; Braddick 1980) is realized by this type of model-based attention tracking. In other words, it relies on sets of attention routines that acquire and track targets (Cavanagh 1992) and it is bounded by the capacity limits and temporal resolution of attention (Verstraten et al. 2000).

WHAT ARE THE SPATIOTEMPORAL LIMITS OF DYNAMIC ATTENTION AND HOW DO THEY DIFFER FROM THOSE OF STATIC ATTENTION?

The importance of mobile attention for perceiving a dynamic scene is revealed when viewing a display created by Holcombe, Linares, and Vaziri-Pashkam (2011). Two circular arrays of coloured patches, centred on fixation, revolved continuously at the same rate. In the example shown in Fig. 23.2, the green patch in the inner ring is always aligned with the red patch in the outer ring. At slow rotation rates, that spatial relation (green aligned with red) is easy to perceive, as are the relative positions of all the other objects. However, above about 1.5 revolutions per second, one can no longer see which colours are adjacent. Yet the colours present are still easily recognized, and the motion direction easily perceived. The speed limit for attentionally tracking a single disc is approximately equivalent to that for judging their spatial relations. This is unlikely to be a coincidence, and this limit and other evidence (Holcombe et al. 2011; Franconeri, Scimeca, Roth et al. 2011) indicate that attentional tracking is required to perceive spatial relationships. Attentional tracking allows one to select an individual object with attention, which is required to apprehend its spatial relationships with other objects, possibly by shifting attention among them (Holcombe et al. 2011; Franconeri et al. 2011). The temporal limits on selection that constrain this process are reviewed below.

The temporal limits for attention are quite severe (Holcombe 2009; Shapiro this volume) and they are already in evidence for a stimulus that changes in place without moving. The shortest duration that can be isolated with attention within a stream of events has been called the dwell time of attention (Duncan, Ward, and Shapiro 1994; Moore, Egeth, Berglan, and Luck 1996). If two events fall within that time, they are irretrievably combined—they cannot be individuated. This duration is reported variously as 150 to 250 ms (Duncan et al. 1994; Moore et al. 1996). This same temporal limit constrains attention when a target moves. For example, if a dot turns off at one location and a second one turns on at a different location, observers report the apparent motion of a single target. If the two dots continue to alternate at the two locations, the impression of a dot moving back and forth is compelling as long as the rate of alternation remains under 5 to 8 Hz (equivalent to dwell times of 125 to 200 ms). Above that rate, the on and off phases

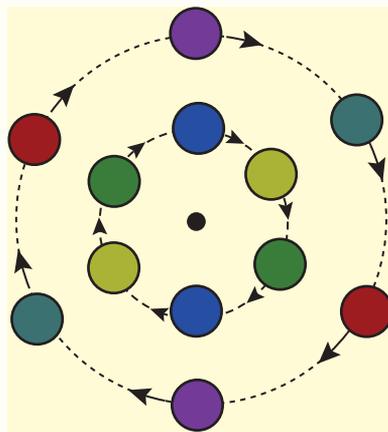


FIGURE 23.2 Spatial judgements between moving targets require attentive tracking. The coloured discs revolve about fixation, all at the same rate. Thus, two colours that are adjacent remain adjacent throughout the display. Above the speed limit for attentional tracking, however, observers are unable to judge which colours are adjacent.

for each dot are no longer resolved and so cannot be compared from the first dot to the second, making it impossible to check whether the offset of the first is coincident with the onset of the second, an essential requirement for seeing motion. Without this timing information the ‘correspondence problem’ cannot be solved, the offset of one dot cannot be linked to the onset of the other. The two locations now appear as two separate, flickering dots rather than one dot in motion (e.g. Anstis, Giaschi, and Cogan 1984: their Fig. 23.4b).

In temporal terms, the limits for selection of a static and a moving target are similar—attention has the same ‘dwell time’ in both cases. However, where they differ is in how the dwell time is spread over space. Specifically, in the static case, attention remains at a fixed location and requires about 200 ms to individuate single events at that location. However, in the moving case, as we will describe below, attention at any one location along the path can access events as brief as 50 ms (Cavanagh, Holcombe, and Chou 2008). The dwell time is spread out along the spatiotemporal path and moving attention can select brief stimuli along the path that could not otherwise be individuated.

Unlike recognition of certain elementary features that can be perceived at very fast rates of over 20 per second (Holcombe 2009), the maximum rate at which a single item can be recognized in a rapid sequence is around 10–12 items per second, or 5–6 Hz (White and Harter 1969; Potter 1993; Vagharchakian, Dehaene-Lambertz, Pallier, and Dehaene 2012). This limit is the same if the information is presented alternately to each eye, suggesting that the limitation is not due to peripheral constraints, but the temporal resolution of attention (White, Cheatham, and Armington 1953; Andrews, White, Binder, and Purves 1996). As well as limiting performance in rapid-serial-visual-presentation (RSVP) tasks that involve rapid presentation of individual objects, this maximum rate can also constrain discriminations of the relations

between simultaneously presented simple features. Temporal rates for phase discrimination of flickering lights show this low temporal limit (He, Intriligator, Verstraten, and Cavanagh 1998; He and MacLeod 1996; Rogers-Ramachandran and Ramachandran 1998). These and other data have led several authors to propose both a slow and a fast mechanism for detecting phase differences (Rogers-Ramachandran and Ramachandran 1998; Forte, Hogben, and Ross 1999; Victor and Conte 2002) where the fast mechanism can only work over short distances whereas the slow mechanism can operate over very large distances. The temporal limit of the slow mechanism has been linked to the temporal resolution of attention where the individuation of the light and dark phases of the flicker is likely to be mediated by visual attention (Battelli, Cavanagh, Martini, and Barton 2003a; Verstraten et al. 2000; Aghdaee and Cavanagh 2007). Note that this temporal limit is much lower than the temporal resolution of vision, which is around 30–50 Hz (Andrews et al. 1996; Rovamo and Raninen 1984; see review Holcombe 2009). Thus, just as the spatial resolution of attention is much worse than the spatial resolution of vision (Intriligator and Cavanagh 2001), the temporal resolution of visual attention is also much coarser than the temporal resolution of vision.

Similar limits are found for high-level motion tasks. Whereas simple luminance-defined motion can be perceived at fast rates of over 30 Hz (Burr and Ross 1982), for tracking a target in ambiguous motion (Verstraten et al. 2000; Battelli, Cavanagh, Intriligator et al. 2001), or in apparent motion (Verstraten et al. 2000), or a bar in a continuously drifting, sinusoidal grating, the upper rate for tracking is about 4–8 Hz (Verstraten et al. 2000). In their test with continuously moving targets, there was also an indication of a maximum speed for tracking of about 2 rotations per second (about the fovea). The limiting rate of 4–8 Hz is quite close to the well-documented limits on apparent motion (more specifically, at this rate and spacing, phi motion, Neuhaus 1930; Caelli and Finlay 1979, 1981; Tyler 1973), on phase discrimination of flickering lights (He and MacLeod 1996; He et al. 1998; Rogers-Ramachandran and Ramachandran 1998), on motion of drifting stereo-defined and motion-defined gratings (Patterson, Ricker, McGary, and Rose 1992; Lu and Sperling, 1995), and on smooth pursuit for sampled motion (Morgan and Turnbull 1978). These phenomena may all be limited by a common factor: the temporal resolution of attention.

Battelli, Pascual-Leone, and Cavanagh (2007) proposed that the limiting factor is the access to the individual events in a rapid stream of events. In the case of ambiguous or apparent motion, each disc in the display is turning on and off and the task is to pair the offset of one disc with the onset of the next, adjacent disc. If each disc is turning on and off very rapidly, it is possible that the relative timing of the offsets and onsets of different discs is no longer available, making it impossible to judge if one disc turns on at about the same time as the other turns off, a requirement for combining the two discs in the perception of a single disc in motion. At low rates of flicker, say, 1 or 2 Hz, an individual disc appears to turn on and turn off at discrete moments. Tracking at these rates is relatively easy. At higher rates of flicker, the same disc may appear to be continuously present but flickering—there is no access to the separate on and off intervals, and no way to link the offset of one disc to the onset of the neighbouring disc. Tracking fails at these rates, 4–8 Hz and higher.

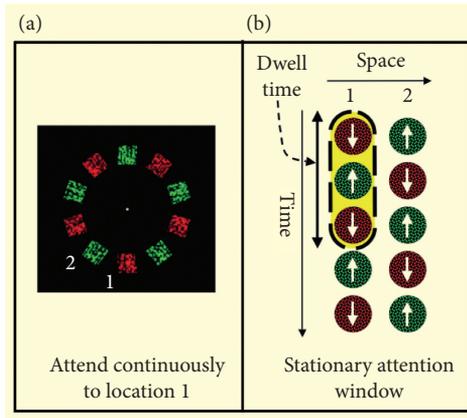


FIGURE 23.3 Attention sampling from a fixed location. (a) Each coloured, moving texture patch switches between red inward motion and green outward motion. (b) When attention is focused on location 1, sampling information from that patch, it has a minimum duration or dwell time before it can stop sampling, typically no less than 200 msec (Theeuwes, Godijn, and Pratt 2004; Duncan, Ward, and Shapiro 1994). During that time, the patch alternates between the two values and the resulting mixture degrades the ability to pair the colours with their motions. Adapted from *Journal of Vision*, 8(12), article 1, Cavanagh, P., Holcombe, A. O., & Chou, W., Mobile computation : spatiotemporal integration of the properties of objects in motion, pp. 1–23, figure 13 (2008), The Association for Research in Vision and Ophthalmology.

In one tracking experiment (Verstraten et al. 2000: experiment 3), the stimuli were in continuous motion, so low-level motion signals were available. The direction of the rotation of the grating could be reported at much faster rates than the 4–8 Hz where tracking failed. Just as some mechanism exists that responds to flicker even when separate on and off intervals are no longer experienced, some mechanism exists, undoubtedly low-level direction-selective units, that responds to motion at rates beyond those that support tracking individual targets.

We return now to the dwell time of attention. This refers to the minimum temporal interval that can be attended independently of preceding and following stimulation (Duncan et al. 1994). The dwell time for selecting and combining the colours and motions is fairly long, 300 ms or more (Moradi and Shimojo 2004; Arnold 2005), as it is for other attention-dependent tasks (e.g. Duncan et al. 1994; Holcombe and Cavanagh 2001). In an experiment by Cavanagh, Holcombe, and Chou (2008), colours and motion were alternated rapidly at each location in an array. At higher rates of alternation, 4 Hz or more, both of the alternating colours and both of the alternating motions are present within the dwell time (Fig. 23.3) so that processing of the colour–motion combination cannot be completed before the next pair arrives. Performance was severely degraded for rates above 3 Hz as would be expected from the standard view of attentional dwell time.

However, quite different results were seen when attention was moving. Figure 23.4 shows the alternating displays and the sampling window for attention as it moves across locations when the display is constructed so that each successive patch acquired

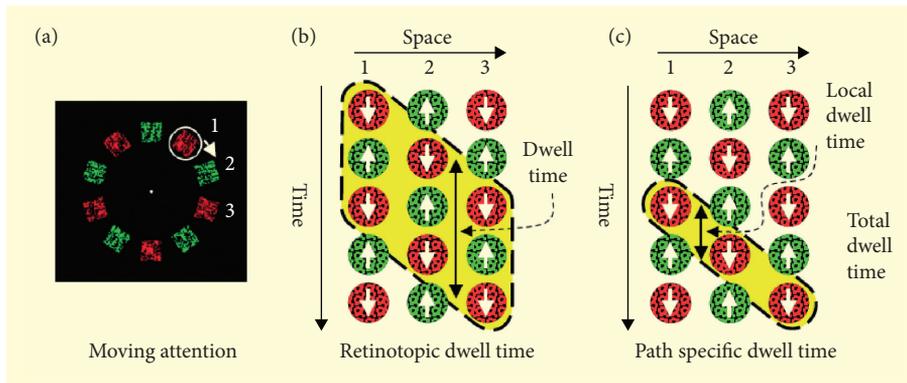


FIGURE 23.4 Attention sampling from a moving location. (a) On the simple dwell time account, when attention is moving over the alternating patches, it opens an attention window at each location that stays open for the dwell time before closing again. (b) With this simple dwell time theory, alternating stimuli at each location would be integrated to the same extent whether attention is moving or stationary. (c) The results instead showed that moving attention can offer substantial performance advantages, suggesting that once attention starts sampling at a given location, it does not continue to sample there for the whole dwell time, but rather it samples along the trajectory of motion. It may access a given location only very briefly (local dwell time as little as 50 ms), allowing attention to sample brief instants from a rapidly changing stream whose elements would otherwise be inaccessible to attention. Reproduced from *Journal of Vision*, 8(12), article 1, Cavanagh, P., Holcombe, A. O., & Chou, W., Mobile computation : spatiotemporal integration of the properties of objects in motion, pp. 1–23, figure 14 (2008), The Association for Research in Vision and Ophthalmology.

by moving attention is the same. Performance improved dramatically, indicating that attention no longer dwelled at a single location for an extended period, but rather its ≈ 300 ms dwell time is spread over different locations at different times so that it continually samples a single colour–motion pairing. It seems that when attention is moving, the dwell time is spread over space, covering 8° to 12° of visual angle at an eccentricity of 6.5° for the speeds used in that experiment. At even higher speeds, access by attention to any one location (local dwell time) may last as little as the 50 msec. The implication is that once attention arrives at a location and opens a channel to sample information from that position, that sampling channel is not local but moves on as attention moves on. It does not remain open for the full 300 ms at that location once attention has moved on.

WHAT ARE THE ANATOMICAL UNDERPINNINGS OF DYNAMIC ATTENTION?

Two distinctive properties characterize spatial attention and distinguish it from dynamic, spatiotemporal attention. First, a wide variety of imaging, patient, and normal behavioural studies have shown that the networks controlling visual spatial attention, in

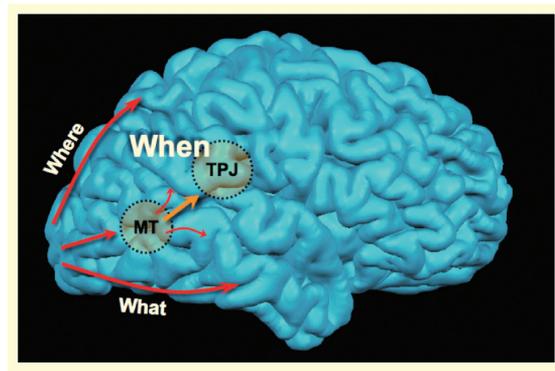


FIGURE 23.5 The ‘When’ pathway. Studies on neglect patients and TMS on normals suggest that there is a right parietal centre for interpreting the temporal order of events on the sub-second scale. This right hemisphere centre analyses temporal events in both hemifields.

the dorsal frontal and parietal areas (Battelli et al. 2001; Corbetta and Shulman 2002; see Corbetta and Shulman 2011 for a review), are generally contralaterally organized. That is, areas in the right hemisphere oversee spatial attention in the left visual field and vice versa. Second, the acuity of spatial attention scales with eccentricity. We can pay attention to, and select in isolation very small targets among closely spaced distractors when they are near the fovea but as targets move into the periphery, the spacing required for individual selection gets very large very quickly (Intriligator and Cavanagh 2001).

In contrast, the right hemisphere has a special role in the control of temporal aspects of dynamic attention for discrete stimuli and it appears to be bilaterally organized (Fig. 23.6, Battelli et al. 2001, 2003a, 2007, 2008). The temporal aspect that we focus on is the sorting and ordering of transients into the meaningful structure of an event stream. Objects appear, move, and disappear and all of these changes produce transients that on their own are not very informative. They need to be grouped together so an onset at one location and an offset at another are seen as the motion path of a single object. Each object on its own also needs to be individuated from preceding and following objects. The ability to individuate single events in a rapidly changing stream can be seen as a temporal equivalent to spatial acuity, as discussed in the previous section. But the temporal limit for the individuation of events as separate rather than an unintelligible flicker is much lower. This ability to detect the order of events, whether two events are seen as simultaneous or successive, sets the stage for the moment-to-moment interpretation of the visual world. Evidence from parietal patients, functional magnetic resonance imaging (fMRI), and TMS of the parietal lobe suggests that the right parietal lobe underlies this analysis of event timing for events in both left *and* right visual fields. Judgement of temporal order, simultaneity, and high-level motion (Fig. 23.6) are all impaired after right parietal lesions, but not left (Rorden et al 1997; Battelli et al. 2003a; Reddy, Rémy, Vayssière, and VanRullen 2011) and degraded after TMS over the right inferior parietal lobe (VanRullen, Pascual-Leone, and Battelli 2008). The experimental evidence suggests that the right inferior parietal lobe serves as part of a *when* pathway that mediates the timing component of many sensory capabilities from visual to auditory object discrimination across time (Rauschecker 2011).

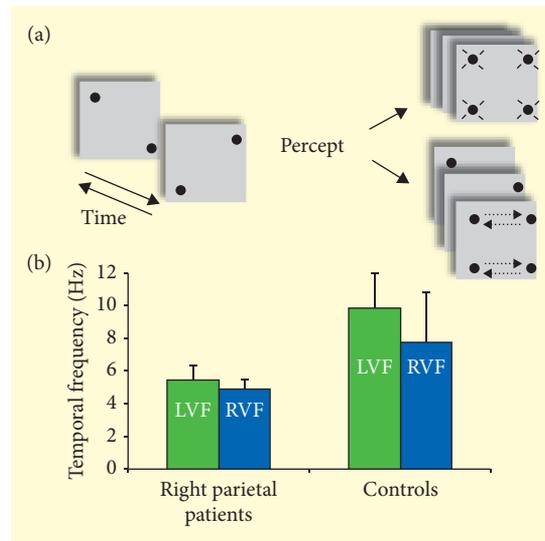


FIGURE 23.6 Bilateral impairment in apparent motion. (a) A quartet apparent motion stimulus. Two frames with two dots each are alternated at a variable frequency (left, arrows indicate alternation in time). When the interval between the frames is very short (at high frequency, more than 10 Hz), subjects can perceive only flickering dots and no motion is reported (top right). At appropriate time intervals (around a frequency of alternation of 7 or 8 Hz), subjects report motion (bottom right). (b) Patients who have right parietal lesions (average data from three patients) show a severe deficit in perceiving apparent motion both in the left visual field (LVF) and in the right visual field (RVF). Their threshold is about half that of normal controls (average of six age-matched controls are reported). The patients cannot distinguish between four flashing and two moving dots unless the alternation rate is as low as 4 or 5 Hz, which corresponds to an average of 200 ms interval between frames. Reprinted from *Trends in Cognitive Sciences*, 11(5), Lorella Battelli, Alvaro Pascual-Leone, and Patrick Cavanagh, The ‘when’ pathway of the right parietal lobe, pp. 204–10, Copyright (2007), with permission from Elsevier.

In addition, the temporal resolution of attention does not appear to change much with eccentricity (Aghdaee and Cavanagh 2007), decreasing only moderately in the periphery. The *spatial* resolution of attention varies dramatically across the visual field; a variation may arise from the properties of the cortices where attention operates. The underlying assumption is that an ‘attentive field’ has a constant size on the visual cortex on which it operates, so that the scaling of the attentional field with eccentricity reflects the cortical magnification factor of that particular cortex. Parietal areas are often implicated in the control of spatial attention (Culham et al. 1998; Posner, Walker, Friedrich, and Rafal 1984, 1987). There is no corresponding temporal cortical magnification factor yet identified. The flicker fusion rate does not vary much across the visual field either as a function of eccentricity or as a function of visual field (upper vs. lower) (Rovamo and Raninen 1984), although the spatial integration area that sets it does (Granit and Harper 1930). This suggests that the temporal resolution of low-level (visual) mechanisms is relatively homogeneous across the visual field. Aghdaee and Cavanagh (2007) showed

that high-level (attentional) resolution was relatively unchanged with eccentricity as well. They measured the temporal resolution of attention using long-range phase judgments, based on the assumption that attention is required to individuate the phases of spatially widely separated flickering stimuli. They concluded that the variation of the temporal limits of visual attention across the visual field differs markedly from that of the spatial resolution of attention.

Battelli et al. (2007) demonstrated another loss in temporal processing for detecting an odd item, a white square among black squares where all the squares alternate together in contrast, white to black and black to white. We might imagine that the odd square should be easy to notice as a single white square 'pops out' among black squares and vice versa. However, just as the 'effortless' processing of biological motion turned out to require attention (Cavanagh et al, 2001), so too does the discrimination of the 'odd' contrast item in an alternating display. In particular, a patient with a right parietal lesion is severely impaired at this task unless the alternation rate is below 3 Hz, while normal subjects fail on the task at alternation rates above 7/8 Hz (Fig. 23.7).

Patients appear to be able to discriminate temporal changes of objects with a much lower resolution relative to healthy subjects and studies with normal subjects and cerebrally lesioned patients show that brain regions in the parietal lobe are involved in the analysis of time as well as space, for both visual (Husain, Shapiro, Martin, and Kennard 1997; Battelli et al. 2001; Hillstrom, Husain, Shapiro, and Rorden 2004) and auditory (Rao, Mayer, and Harrington 2001; Harrington, Haaland, and Knight 1998) stimuli (see Husain and Rorden 2003, for a review). Studies with non-human primates are consistent with this view (Janssen and Shadlen, 2005; Herrington and Assad 2009, 2010) and they demonstrate the role of the monkey lateral intraparietal sulcus (LIP) in orienting of attention to sudden change of events in time. The human homologue of monkey LIP is presumably part of the posterior portion of the inferior parietal lobe (Orban, Claeys, Nelissen et al. 2006) and this brain area plays a major role in detecting visual events at unexpected locations (Kincade, Abrams, Astafiev et al. 2005). In particular, studies on patients with lesions in the right inferior parietal lobe suggest a specific role for this area of the brain in perceptual abilities that require the analysis of time (Husain et al. 1997; Magnani, Oliveri, Mancuso et al. 2011).

A fMRI (Claeys, Lindsey, De Schutter, and Orban 2003) study has demonstrated that the right inferior parietal lobe is significantly more active while perceiving a stimulus moving in apparent motion compared to the same dots flashing at identical frequency. The authors used the same stimulus we used with parietal patients and their results were in very good agreement with our data (Fig. 23.5, from Battelli et al. 2001). Furthermore another fMRI study has shown more significant activity in the right inferior parietal lobe while subjects were asked to covertly orient visual attention toward sudden visual stimuli (Yantis, Schwarzbach, Serences et al. 2002) and a similar result was also obtained in an MEG study (Martinez-Trujillo, Cheyne, Gaetz et al. 2007) where subjects were asked to report a transient change in speed in a moving random dot pattern in the left or in the right visual field. An EEG study (VanRullen, Reddy, and Koch 2006) showed a correlation between EEG signal in the right parietal lobe and the illusory perception of a rotating wheel that required discrete motion processing. TMS studies have also shown

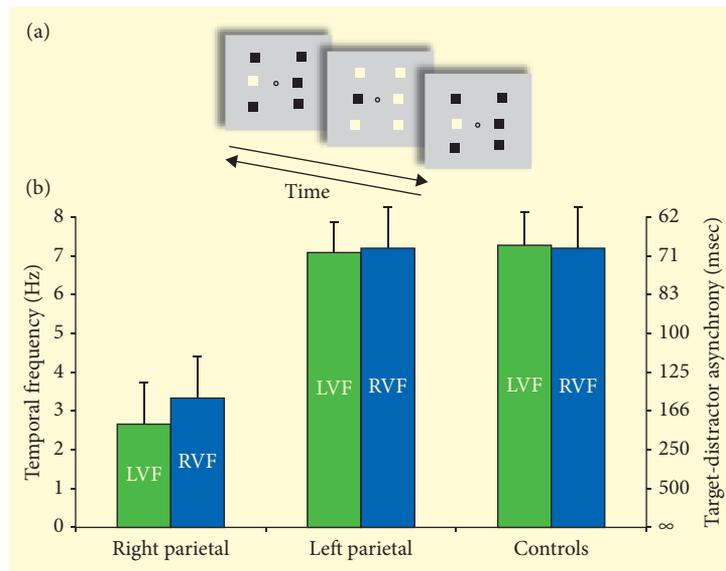


FIGURE 23.7 Phase discrimination task: bilateral deficit of identification of a visual event. (a) Subjects were asked to identify the odd target among six squares that alternated black and white at the same frequency as the target (middle item in the column left of fixation, top panel; arrows indicate alternation in time). The phase of the target square was shifted in time relative to the other five squares (when the target was black, the distractors were white). The target is easily seen at low alternation rates, but the task becomes more difficult at high alternation rates (for demonstrations of the task and patients' performance, see <http://visionlab.harvard.edu/Members/Lorella/movies/movies.htm>). (b) Normal controls and patients who had left parietal lesions could perform the task up to a speed of 7 or 8 Hz, whereas patients who had right parietal lesions had a threshold speed of 3 Hz for both the left visual field (LVF) and the right visual field (RVF). Asynchrony (ms) between the target and the distractors is reported on the right axis. Reprinted from *Trends in Cognitive Sciences*, 11(5), Lorella Battelli, Alvaro Pascual-Leone, and Patrick Cavanagh, The 'when' pathway of the right parietal lobe, pp. 204–10, Copyright (2007), with permission from Elsevier.

that the right parietal lobe must be specialized in performing tasks requiring the discrimination of discrete events in visual and auditory timing (Beck, Muggleton, Walsh, and Lavie 2006; Alexander, Cowey, and Walsh, 2005). Finally, a recent fMRI study (Reddy et al. 2011) showed activity in the right parietal lobe during the illusory perception of a rotating wheel that required discrete motion processing. The activity was independent of the side of stimulus presentation. Moreover, a TMS study using the same stimuli (VanRullen, Pascual-Leone, and Battelli, 2008) confirmed the role of the right inferior parietal lobe in perceiving the spatiotemporal structure of events, in this case discriminating forward from reverse motion. Altogether these data show evidence of a special role of the right inferior parietal lobe in visual event timing using both non-spatially lateralized dynamic and stationary stimuli.

From these studies, Battelli et al. (2007) concluded that the deficit involves the accuracy in parsing offsets and onsets as belonging to or not belonging to the same event. If

the structure of offsets and onsets could not be paired together at higher rates, it would not be possible to link the offset of one dot with the onset of the other as a single item in motion. Note that the patients perceive smooth motion normally and show deficits only in the contralesional visual field in other attention-related motion tasks (Battelli et al. 2001).

DOES DYNAMIC ATTENTION HAVE A TEMPORAL STRUCTURE?

Increasing evidence suggests that attention can concurrently select multiple locations (e.g. Pylyshyn and Storm 1988), yet it is not clear whether this ability relies on continuous allocation of attention to the different targets (a 'parallel' strategy) or whether attention switches rapidly between the targets (a periodic 'sampling' strategy). With respect to visual search tasks, in which a single target must be detected among a variable number of elements, this debate has divided the community for quite some time, with no accepted conclusion. A similarly unresolved argument has been made regarding multiple-object tracking paradigms (Tripathy, Ogmen, and Narasimhan 2011).

A recent article by VanRullen, Carlson, and Cavanagh (2007) addressed this question in a task where a 'probe' event of variable duration was detected by the observer. When only a single location was cued, the observer could allocate their attentional resources entirely to this location ('full attention' condition). In other trials, there were two or more cued locations ('divided attention'). Finally, on catch trials, the probe occurred on an uncued, unexpected location ('minimal attention' condition). Within a 'parallel' model, attention is shared across the targets so performance for a given probe duration should lie somewhere between the performance levels obtained with full and with minimal attention at this same duration. As the number of cued locations increases, the performance should move uniformly closer to the function found for minimal attention. For a 'sampling' strategy, however, performance with any given target could be at the full or minimal attention level depending on the location of attention. This latter case is what was found.

These results showed that attention might resolve a difficult, attentionally demanding task by periodically sampling information from the different target locations, at a rate of approximately seven elements per second. A related study by Landau and Fries (2012) has provided further support. The results also indicated that attention operated with periodic sampling even when it was focused on a single target location. If attention, when focused on a single location, samples information periodically like a blinking spotlight, then why did hundreds of previous studies of attentional mechanisms not reveal this property? The fact that most experimental paradigms (even those involving electrophysiology) rely on averaging signals across several trials is probably one reason. If the onset of each periodic attentional sample (an internal process) bears no relation to

stimulus onset (an external event), such averaging would conceal the effects of periodic attentional sampling from the experimenter.

It is nevertheless puzzling that attention should sample cyclically when only one location is attended. Periodic sampling is often seen in sensory systems: saccades in vision, sniffs in olfaction, whisker movements in rat somatosensation, and even echolocation in bats or electrolocation in electric fish are all examples of explicit cycling of perceptual uptake (Uchida, Kepecs, and Mainen, 2006). Attentional sampling might have evolved from these periodic processes. There may also be multiple stages in sampling that require periodic breaks in uptake from an attended stimulus. Perhaps sampling must alternate with transmission or other control processes. Whatever the reason, the long debate over serial versus parallel processing will continue for the question of attention itself.

IS THERE A SALIENCE MAP OF LOCAL TIME THAT IS SOMETIMES DISTORTED BY STRONG ATTENTIONAL FOCUS?

A number of studies report that the subjective experience of time is slowed at traumatic or attention-grabbing events (see review, Eagleman 2008). One interpretation of this phenomenon is that perceived duration is a function of the amount of information processed per unit of objective time. Attention may boost the amount of information processed above baseline level so that it generates more information per unit of objective time (Fig. 23.8). Consequently, the attended event may seem to last longer than a less attended event of the same objective duration. Tse, Intriligator, Rivest, and Cavanagh (2004) used an oddball paradigm to explore this phenomenon. A stream of repeating stimuli were presented, one per second for example, each lasting 500 ms (these durations were varied). Occasionally a novel item was presented and subjects had to adjust its duration until it appeared to last as long as the repeating stimulus. Overall, the novel item appeared to last 50% longer. More extreme versions of this experiment were conducted by Stetson and his colleagues (Stetson, Fiesta, and Eagleman 2007) where subjects were released from a tall tower for 50 metres (3 seconds) of freefall (into a net). They again judged the interval as longer than a control (non-terrifying) interval that was matched in objective time. Stetson et al. tried to test whether this expansion of time was accompanied by a greater amount of information processed per unit of time, using a test related to measurement of flicker fusion rate. However, the lack of eye movement controls for the rapidly falling observers compared to the calmly sitting observers leaves the question regarding flicker fusion unresolved. Additional tests should also be done on the rate of processing at rates beyond the flicker fusion limit.

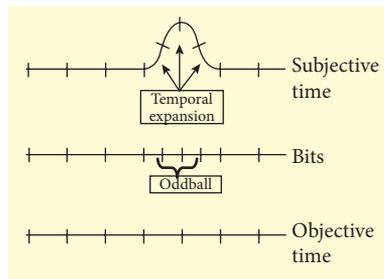


FIGURE 23.8 Attention-induced, time dilation. When an attention-grabbing event occurs, more information is processed over the stimulus per unit of objective time. If subjective time is gauged in terms of the amount of perceptual information processed, subjective time will seem to expand relative to objective time, as shown at the top region indicated ‘temporal expansion’. Reproduced from *Perception & Psychophysics*, 6(7), 2004 pp 1171–1189, Attention and the subjective expansion of time, Tse, P., Intriligator, J., Rivest, J., and Cavanagh, P., © Springer Science and Business Media. With kind permission from Springer Science and Business Media.

CONCLUSIONS

We reviewed the role of attention in tracking and processing dynamic events. We showed that attention has a mobile point of operation or ‘pointer’ that follows moving targets, picking up pieces of evidence along the way to determine not just what a target is, but what it is doing. Familiar trajectories help identify a target and guide encoding of continuing input from its path. Attention has coarse temporal resolution but when the focus of selection is on the move, a given location on a moving target’s path can be selected for as little as 50 ms, compared to the typical ‘dwell time’ or minimum duration of attention selection at a fixed location of 200 ms or more. This indicates that the temporal capacity limits of attention are imposed in a target-specific frame of reference, not a retinal coordinate frame. When individuating targets in a rapidly changing scene, a critical limit is the necessity to assess each transient as a target offset or an onset. This is not as simple as encoding and cataloguing luminance transients because the onset of an object that is darker than its surround will produce a decrement in luminance whereas the onset of an object that is lighter than its surround will produce an increment. Instead, objects must be segmented, identified, and tracked, a process that is slower than simple detection of transients by a factor of about 10. This step of temporal selection is fundamental in our rich visual environment where suddenly appearing (and disappearing) salient objects must be continually and rapidly discriminated from the background. This process has been localized to the right parietal region, a cortical structure that was then seen as a central part of a ‘when’ pathway. Patient studies show that this temporal selection is a qualitatively different system from spatial attention, where right parietal patients affected by neglect show a strong spatial impairment in the contralateral hemifield *only*. In contrast, this temporal selection and tracking of object identity is completely based in the right inferior parietal lobe for events in both hemifields.

Finally, attention may have a cyclical nature, sampling its input, whether static or dynamic, in a series of snapshots at a preferred sampling rate of around 8 Hz, and may be able to allocate more resources to upcoming moments of expected salience, with one consequence being a dilation in the subjective experience of time during those moments.

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REFERENCES

- Aghdaee, S. M. and Cavanagh, P. (2007). Temporal limits of long-range phase discrimination across the visual field. *Vision Research* 47: 2156–2163.
- Alexander, I., Cowey, A., and Walsh, V. (2005). The right parietal cortex and time perception: Back to Critchley and the Zeigler phenomenon. *Cognitive Neuropsychology* 22: 306–315.
- Alvarez, G. A. and Franconeri, S. L. (2007). How many objects can you track? Evidence for a resource-limited attentive tracking mechanism. *Journal of Vision* 7(13): 14.1–10.
- Andrews, T. J., White, L. E., Binder, D., and Purves, D. (1996). Temporal events in cyclopean vision. *Proceedings of the National Academy of Sciences USA* 93(8): 3689–3692.
- Anstis, S. M. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 290: 153–168.
- Anstis, S., Giaschi, D., and Cogan, A. I. (1984). Adaptation to apparent motion. *Vision Research* 25: 1051–1062.
- Arnold, D. H. (2005). Perceptual pairing of colour and motion. *Vision Research* 45: 3015–3026.
- Ballard, D. H., Hayhoe, M. M., Pook, P. K., and Rao, R. P. (1997). Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences* 20: 723–742; discussion 743–767.
- Bartlett, S. F. (1932). *Remembering: A Study in Experimental and Social Psychology*. Cambridge: Cambridge University Press.
- Battelli L., Alvarez G., Carlson T., and Pascual-Leone A. (2009). The role of the parietal lobe in visual extinction studied with transcranial magnetic stimulation. *Journal of Cognitive Neuroscience* 21(10): 1946–1955.
- Battelli, L., Cavanagh, P., Intriligator, J., Tramo, M. J., Hénaff, M.-A., Michèl, F., and Barton, J. S. (2001). Unilateral right parietal damage leads to bilateral deficit for high-level motion. *Neuron* 32: 985–995.
- Battelli, L., Cavanagh, P., Martini, P., and Barton, J. S. S. (2003a). Bilateral deficits of transient visual attention in right parietal patients. *Brain* 126: 2164–2174.
- Battelli, L., Cavanagh, P., and Thornton, I. M. (2003b). Perception of biological motion in parietal patients. *Neuropsychologia* 41(13): 1808–1816.
- Battelli, L., Pascual-Leone, A., and Cavanagh, P. (2007). The 'when' pathway of the right parietal lobe. *Trends in Cognitive Science* 11: 204–210.

- Battelli, L., Walsh, V., Pascual-Leone, A., and Cavanagh, P. (2008). The 'when' parietal pathway explored by lesion studies. *Current Opinion in Neurobiology* 18: 120–126.
- Beck, D. M., Muggleton, N., Walsh, V., and Lavie, N. (2006). Right parietal cortex plays a critical role in change blindness. *Cerebral Cortex* 16(5): 712–717.
- Braddick, O. (1974). A short-range process in apparent motion. *Vision Research* 14: 519–527.
- Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society Biological Sciences*, 290: 137–151.
- Burr, D. C. and Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research* 22: 479–484.
- Caelli, T. and Finlay, D. (1979). Frequency, phase, and colour coding in apparent motion. *Perception* 8: 59–68.
- Caelli, T. and Finlay, D. (1981). Intensity, spatial frequency, and temporal frequency determinants of apparent motion. *Perception* 10: 183–189.
- Cavanagh, P. (1992). Attention-based motion perception. *Science* 257: 1563–1565.
- Cavanagh, P. and Alvarez, G. (2005). Tracking multiple targets with multifocal attention. *Trends in Cognitive Sciences* 9: 349–354.
- Cavanagh, P., Holcombe, A. O., and Chou, W. (2008). Mobile computation: Spatiotemporal integration of the properties of objects in motion. *Journal of Vision* 8(12): 1.1–23.
- Cavanagh, P., Hunt, A., Afraz, A., and Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences* 14: 147–153.
- Cavanagh, P., Labianca, A. T., and Thornton, I. M. (2001). Attention-based visual routines: Sprites. *Cognition* 80: 47–60.
- Claeys, K. G., Lindsey, D. T., De Schutter, E., and Orban, G. A. (2003). A higher order motion region in human inferior parietal lobule: Evidence from fMRI. *Neuron* 40(3): 631–642.
- Corbetta, M. and Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience* 3(3): 201–215.
- Corbetta, M. and Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience* 2011(34): 569–599.
- Culham, J. C., Brandt, S. A., Cavanagh, P., Kanwisher, N. G., Dale, A. M., and Tootell, R. B. H. (1998). Cortical fMRI activation produced by attentive tracking of moving targets. *Journal of Neurophysiology* 80: 2657–2670.
- Culham, J. C., Cavanagh, P., and Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas with fMRI activation during parametric variations of attentional load. *Neuron* 32: 737–745.
- Drew, T., McCollough, A. W., Horowitz, T. S., and Vogel, E. K. (2010). Attentional enhancement during multiple-object tracking. *Psychonomic Bulletin & Review* 16(2): 411–417.
- Duncan, J., Ward, R., and Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature* 369: 313–315.
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinions in Neurobiology*, 18(2):131–136. doi: 10.1016/j.conb.2008.06.002.
- Forte, J., Hogben, J. H., and Ross, J. (1999). Spatial limitations of temporal segmentation. *Vision Research* 39(24): 4052–4061.
- Franconeri, S. L., Scimeca, J. M., Roth, J. C., Helseth, S. A., and Kahn, L. E. (2011). Flexible visual processing of spatial relationships. *Cognition* 122(2): 210–227.
- Freeman, T. C. and Banks, M. S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research* 38: 941–945.
- Granit, R. and Harper, P. (1930). Comparative studies on the peripheral and central retina. II: Synaptic reactions in the eye. *American Journal of Physiology* 95: 211–228.

- Harrington, D. L., Haaland, K. Y., and Knight, R. T. (1998). Cortical networks underlying mechanisms of time perception. *Journal of Neuroscience* 18(3): 1085–1095.
- He, S. and MacLeod, D. I. (1996). Local luminance nonlinearity and receptor aliasing in the detection of high-frequency gratings. *Journal of the Optical Society of America A: Optics, Image Science, and Vision* 13(6): 1139–1151.
- He, S., Intriligator, J., Verstraten, F. A. J., and Cavanagh, P. (1998). Slow mechanism for phase discrimination of both luminance and color flicker. *Investigative Ophthalmology and Visual Science* 39: 1110 (suppl).
- Herrington, T. M. and Assad, J. A. (2009). Neural activity in the middle temporal area and lateral intraparietal area during endogenously cued shifts of attention. *Journal of Neuroscience* 29(45): 14160–14176.
- Herrington, T. M. and Assad, J. A. (2010). Temporal sequence of attentional modulation in the lateral intraparietal area and middle temporal area during rapid covert shifts of attention. *Journal of Neuroscience* 30(9): 3287–3296.
- Hillstrom, A. P., Husain, M., Shapiro, K. L., and Rorden, C. (2004). Spatiotemporal dynamics of attention in visual neglect: A case study. *Cortex* 40(3): 433–440.
- Hogendoorn, H., Carlson, T. A., and Verstraten, F. A. (2007). The time course of attentive tracking. *Journal of Vision* 7: 2.1–10.
- Holcombe, A. O. (2009). Seeing slow and seeing fast: Two limits on perception. *Trends in Cognitive Sciences* 13(5): 216–221.
- Holcombe, A. O., and Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience*, 4: 127–128.
- Holcombe, A. O. and Chen, W. Y. (2012). Exhausting attentional tracking resources with a single fast-moving object. *Cognition* 123(2): 218–228.
- Holcombe, A. O., Linares, D., and Vaziri-Pashkam, M. (2011). Perceiving spatial relations via attentional tracking and shifting. *Current Biology* 21(13): 1135–1139. doi: 10.1016/j.cub.2011.05.031.
- Horowitz, T. S., Holcombe, A. O., Wolfe, J. M., Arsenio, H. C., and DiMase, J. S. (2004). Attentional pursuit is faster than attentional saccade. *Journal of Vision* 4(7): 585–603.
- Howe, P. D., Horowitz, T. S., Morocz, I. A., Wolfe, J., and Livingstone, M. S. (2009). Using fMRI to distinguish components of the multiple object tracking task. *Journal of Vision* 9(4): 10.1–11.
- Husain, M. and Rorden, C. (2003). Non-spatially lateralized mechanisms in hemispatial neglect. *Nature Reviews Neuroscience* 4(1): 26–36.
- Husain, M., Shapiro, K. Martin, J., and Kennard, C. (1997). Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature* 385(6612): 154–156.
- Intriligator, J. and Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology* 43: 171–216.
- Janssen P. and Shadlen, M. N. (2005). A representation of the hazard rate of elapsed time in macaque area LIP. *Nature Neuroscience* 8(2): 234–241.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics* 14: 201–211.
- Jovicich, J., Peters, R. J., Koch, C., Braun, J., Chang, L., and Ernst, T. (2001). Brain areas specific for attentional load in a motion-tracking task. *Journal of Cognitive Neuroscience* 13: 1048–1058.
- Julesz, B. (1971). *Foundations of Cyclopean Perception*. Chicago: University of Chicago Press.
- Kahneman, D., Treisman, A., and Gibbs, B. J. (1992). The reviewing of object files: Object specific integration of information. *Cognitive Psychology* 24: 175–219.

- Kincade, J. M., Abrams, R. A., Astafiev, A. V., Shulman, G. L., and Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *Journal of Neuroscience* 25(18): 4593–4604.
- Landau, A. N. and Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology* 22(11): 1000–1004. doi: 10.1016/j.cub.2012.03.054.
- Lu, Z.-L. and Sperling, G. (1995). Attention-generated apparent motion. *Nature* 377: 237–239.
- Lu, Z.-L. and Sperling, G. (1996). Three systems for visual motion perception. *Current Directions in Psychological Science* 5: 44–53.
- Magnani, B., Oliveri, M., Mancuso, G., Galante, E., and Frassinetti, F. (2011). Time and spatial attention: Effects of prism adaptation on temporal deficits in brain damaged patients. *Neuropsychologia* 49(5): 1016–1023.
- Martinez-Trujillo, J. C., Cheyne, D., Gaetz, W., Simine, E., and Tsotsos, J. K. (2007). Activation of area MT/V5 and the right inferior parietal cortex during the discrimination of transient direction changes in translational motion. *Cerebral Cortex* 17(7): 1733–1739.
- Minsky, M. (1975). A framework for representing knowledge. In P. H. Winston (ed.), *The Psychology of Computer Vision* (pp. 211–280). New York: McGraw-Hill.
- Moore, C. M., Egeth, H., Berglan, L., and Luck, S. J. (1996). Are attentional dwell times inconsistent with serial visual search? *Psychonomic Bulletin & Review* 3: 360–365.
- Moradi, F. and Shimojo, S. (2004). Perceptual-binding and persistent surface segregation. *Vision Research* 44: 2885–2899.
- Morgan, M. J. and Turnbull, D. F. (1978). Smooth eye tracking and the perception of motion in the absence of real movement. *Vision Research* 18: 1053–1059.
- Neisser, U. (1967). *Cognitive Psychology*. New York: Prentice Hall.
- Neri, P., Morrone M. C., and Burr, D. C. (1998). Seeing biological motion. *Nature* 395: 894–896.
- Neuhaus, W. (1930). Experimentelle Studien über das Schein von Bewegung. *Pflügers Archiv für die Gesamte Psychologie des Menschen und der Tiere* 75: 315–458.
- Orban, G. A., Claeys, K., Nelissen, K., Smans, R., Sunaert, S., Todd, J. T., Wardak, C., Durand, J. B., and Vanduffel, W. (2006). Mapping the parietal cortex of human and non-human primates. *Neuropsychologia* 44(13): 2647–2667.
- Patterson, R., Ricker, C., McGary, J., and Rose D. (1992). Properties of cyclopean motion perception. *Vision Research* 32: 149–156.
- Posner, M. I., Walker, J. A., Friedrich, F. J., and Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal of Neuroscience* 4: 1863–1874.
- Posner, M. I., Walker, J. A., Friedrich, F. A., and Rafal, R. D. (1987). How do the parietal lobes direct covert attention? *Neuropsychologia* 25: 135–145.
- Potter, M. C. (1993). Very short-term conceptual memory. *Memory & Cognition* 21: 156–161.
- Pylyshyn, Z. W. (1989). The role of location indexes in spatial perception: A sketch of the FINST spatial indexing model. *Cognition* 32: 65–97.
- Pylyshyn, Z. W. (2000). Situating vision in the world. *Trends in Cognitive Sciences* 4: 197–207.
- Pylyshyn, Z. W. (2001). Visual indexes, preconceptual objects, and situated vision. *Cognition* 80(1/2): 127–158.
- Pylyshyn, Z. W. and Annan, Jr, V. (2006). Dynamics of target selection in multiple object tracking (MOT). *Spatial Vision* 19(6): 485–504.
- Pylyshyn, Z. W. and Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision* 3: 151–224.
- Ramachandran, V. S. and Anstis, S. M. (1983). Perceptual organization in moving patterns. *Nature* 304(5926): 529–531.

- Ramachandran, V. S. and Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception* 19(5): 611–616.
- Rao, S. M., Mayer, A. R., and Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience* 4(3): 317–323.
- Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research* 271(1–2): 16–25.
- Reddy, L., Rémy, F., Vayssière, N., and VanRullen, R. (2011). Neural correlates of the continuous Wagon Wheel Illusion: A functional MRI study. *Human Brain Mapping* 32(2): 163–170.
- Roelfsema, P. R., Lamme, V. A., and Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 395: 376–381.
- Rogers-Ramachandran, D. C. and Ramachandran, V. S. (1998). Psychophysical evidence for boundary and surface systems in human vision. *Vision Research* 38: 71–77.
- Rorden, C., Mattingley, J. B., Karnath, H. O., and Driver, J. (1997). Visual extinction and prior entry: Impaired perception of temporal order with intact motion perception after unilateral parietal damage. *Neuropsychologia* 35(4): 421–433.
- Rovamo, J. and Raninen, A. (1984). Critical flicker frequency and M-scaling of stimulus size and retinal illuminance. *Vision Research* 24(10): 1127–1131.
- Rubin, N. and Hochstein, S. (1993). Isolating the effect of one-dimensional motion signals on the perceived direction of moving two-dimensional objects. *Vision Research* 3(10): 1385–1396.
- Schank, R. and Abelson R. (1977). *Scripts, Plans, Goals and Understanding*. Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Selfridge, O. G. (1959). Pandemonium: A paradigm for learning. In D. V. Blake and A. M. Uttley (eds.), *Proceedings of the Symposium on the Mechanisation of Thought Processes* (pp. 511–529). London: Her Majesty's Stationery Office.
- Shim, W. M., Alvarez, G. A., Vickery, T. J., and Jiang, Y. V. (2010). The number of attentional foci and their precision are dissociated in the posterior parietal cortex. *Cerebral Cortex* 20(6): 1341–1349.
- Shipley, T. (ed.) (1961). *Classics in Psychology*. New York: Philosophical Library.
- St. Clair, R., Huff, M., and Seiffert, A. E. (2010). Conflicting motion information impairs multiple object tracking. *Journal of Vision* 10(4): 18.1–13.
- Stetson, C., Fiesta, M. P., and Eagleman, D. M. (2007). Does time really slow down during a frightening event? *PLoS One* 2(12): e1295.
- Ternus, J. (1926). Experimentelle Untersuchungen über phänomenale Identität. *Psychologische Forschung* 7: 81–136. [Abridged English translation: Ternus, J. (1938). The problem of phenomenal identity. In W. D. Ellis (ed.), *A Source Book of Gestalt Psychology* (pp. 149–160). London: Routledge & Kegan Paul.]
- Theeuwes, J., Godijn, R., and Pratt, J. (2004). A new estimation of the duration of attentional dwell time. *Psychonomic Bulletin & Review* 11: 60–64.
- Treue, S. and Maunsell, J. H. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382: 539–541.
- Tripathy, S. P., Ogmen, H., and Narasimhan, S. (2011). Multiple-object tracking: A serial attentional process? In C. Mole, D. Smithies, and W. Wu (eds.), *Attention: Philosophical and Psychological Essays* (pp. 117–144). Oxford: Oxford University Press.
- Tse, P., Intriligator, J., Rivest, J., and Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics* 66: 1171–1189.
- Tyler, C. W. (1973). Temporal characteristics in apparent movement: Omega movement vs. phi movement. *Quarterly Journal of Experimental Psychology* 25: 182–192.

- Uchida, N., Kepecs, A., and Mainen, Z. F. (2006). Seeing at a glance, smelling in a whiff: Rapid forms of perceptual decision making. *Nature Reviews Neuroscience*, 7(6): 485–491.
- Vagharchakian, L., Dehaene-lambertz, G., Pallier, C., Dehaene, S., and France, D. (2012). A temporal bottleneck in the language comprehension network. *Journal of Neuroscience* 32(26): 9089–9102. doi: 10.1523/JNEUROSCI.5685-11.2012.
- VanRullen, R., Carlson, T., and Cavanagh, P. (2007). The blinking spotlight of attention. *Proceedings of the National Academy of Sciences USA* 104: 19204–19209.
- VanRullen, R., Pascual-Leone, A., and Battelli, L. (2008). The Continuous Wagon Wheel Illusion and the ‘When’ pathway of the right parietal lobe: A repetitive transcranial magnetic stimulation study. *Plos One* 3(8): e2911.
- VanRullen, R., Reddy, L., and Koch, C. (2006). The Continuous Wagon Wheel Illusion is associated with changes in electroencephalogram power at approximately 13 Hz. *Journal of Neuroscience* 26(2): 502–507.
- Verstraten, F. A. J., Cavanagh, P., and Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research* 40: 3651–3664.
- Victor, J. D. and Conte, M. M. (2002). Temporal phase discrimination depends critically on separation. *Vision Research* 42(17): 2063–2071.
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie* 61: 161–265. Partial English translation in T. Shipley (ed.), *Classics in Psychology* (pp. 1032–1089). New York: Philosophical Library, 1961.
- White, C. T., Cheatham, P. G., and Armington, J. C. (1953). Temporal numerosity. II: Evidence for central factors influencing perceived number. *Journal of Experimental Psychology* 46: 283–287.
- White, C. T. and Harter, M. R. (1969). Intermittency in reaction time and perception, and evoked response correlates of image quality. *Acta Psychologica* 30: 368–377.
- Yantis, S., Schwarzbach J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., and Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience* 5(10): 995–1002.