Linda Lanyon & Susan Denham
Plymouth Institute of Neuroscience
University of Plymouth, UK

Visual search for a target that differs from distracters by a single feature is effortless and parallel. However, when a target is defined by a conjunction of features, a serial search, involving the shifting of an attentional focus, is required [1]. Where eye movements (saccades) are allowed, the attentional focus is shifted overtly and a "scan path" records the locations in the scene selected for fixation. Monkey data [2] indicate that colour is more important than form in driving the scan path during overt visual search for a feature conjunction target defined by its colour and orientation. It is known that lateral intraparietal area (LIP) encodes the location of salient [3] and behaviourally relevant [4,5] features, such as colour, in the scene. This could allow the positions of potential targets to be determined during visual search. Also, it is known that target-coloured features are enhanced in parallel across the visual scene in visual area 4 (V4) from approximately 150ms post-stimulus [6]. Over a similar time course, competition between objects represented in inferotemporal region (IT) is resolved such that the target object is more strongly represented than distracters [7]. Also, increases in baseline activity, thought to be located in area V4, have been observed during human brain imaging when subjects attended to colour even in the absence of coloured stimuli [8]. This is thought to be a result of a top-down bias.

A biased competition computational model of areas V1, V4, IT, LIP and prefrontal cortex (PFC) has been developed to show the development of spatial and object-based attentional effects in V4 and how this could affect the visual search scan path. This model suggests that LIP receives featural information relating to potential targets from extrastriate areas of the ventral stream, for example area V4, which biases spatial competition for the next fixation location. Further, it suggests that certain features (such as colour) are capable, when relevant, of exerting more significant influence on the search scan path than other features (such as form) because of the relative strength of connection to LIP from V4 cells sensitive to these features.

The model operates by moving the retina around the scene. In each retinal image, retinal on-centre, off-surround cells detect colour and luminance. The model V1 contains colour sensitive blob cells and orientation sensitive interblob cells. Areas V4, LIP and IT contain cell assemblies that are modelled using mean field population dynamics [9]. In the V4 module, assemblies selective for colour and orientation receive bottom up inputs from V1. Area IT, containing assemblies selective for the target and distracter objects, receives bottom-up featural inputs from V4 and a top-down bias relating to the target object from PFC. LIP, containing assemblies representing different spatial locations within the retinal image, receives a spatial attentional bias in addition to featural input from V4, which allows LIP to respond to behaviourally relevant features [4,5]

In area V4, competition may be biased by a number of inputs. Spatial attention is able to enhance baseline firing at an early stage (even prior to the first stimulus-invoked response at ~60ms, subsequent to a location cue [10]). The model suggests that a spatial bias, perhaps from a parietal area, is available at an early stage. Object-based attentional effects take longer to develop (beginning at ~150ms post-stimulus following an object cue [11]). The model shows that such object-based effects in V4 require object-related feedback from IT and are dependant on the resolution of competition between objects in IT. The model suggests that an early spatial "attention window" becomes object-based over time as object-related feedback becomes available. This allows the qualitative replication of spatial [10] and object-based [11] attention effects seen in V4. The area within which object-based attention develops and a target can be identified may be constrained by the initial spatial focus of attention, which is set according to stimulus density, as found by [12].

Inhibition of return (IOR) to already inspected locations is a necessary feature of efficient visual search. Parietal damage is linked with a high rate of re-fixation [13]. Saccadic behaviour of an orbitofrontal patient suggests that IOR may be subject to recent associations between sensory/motor events and reward feedback [14]. The model suggests that spatial inhibition of return in the scan path is implemented within parietal cortex (LIP) partly as a result of a scene-based "novelty" (i.e. potential reward) bias, from frontal regions. This means that a scene-based memory trace of locations visited must be available in head-centred coordinates, and that this may need to be mapped to a retinotopic coordinate bias that is applied to an area such as LIP. Such a coordinate transformation may be performed within parietal cortex. This model's resultant active vision scan paths detect target-coloured stimuli across the scene, as found in [2].

[1] Treisman, A. & Gelade, G. (1980) Cognitive Psychology, 12, 97-136
[2] Motter, B. & Belky, E.J. (1998) Vision Research, 38(12), 1805-1815
[3] Gottlieb, J, Kusunoki, M. & Goldberg, M. (1998) Nature, 391, 481-484
[4] Colby, C. L., Duhamel, J. R. & Goldberg, M. E. (1996) Journal of Neurophysiology, 76(5), 2841-2852
[5] Toth, L. & Assad, J. (2002) Nature, 415, 165-168
[6] Motter, B. (1994) The Journal of Neuroscience, 14(4), 2178-2189
[7] Chelazzi, L., Miller, E.K., Duncan, J. & Desimone, R. (1993) Nature, 363, 345-347
[8] Chawla, D., Rees, G. & Friston, K. J. (1999) Nature Neuroscience, 2(7), 671-676
[9] Wilson, H. & Cowan, J. (1972) Biophysics Journal, 12, 1-24
[10] Luck, S, Chelazzi, L, Hillyard, S. & Desimone, R. (1997) Journal of Neurophysiology, 77, 24-42
[11] Chelazzi, L, Miller, E, Duncan, J. & Desimone, R. (2001) Cerebral Cortex, 11, 761-772
[12] Motter, B. & Belky, E. (1998) Vision Research, 38(7), 1007-1022
[13] Husain, M, Mannan, S, Hodgson, T, Wojciulik, E, Driver, J. & Kennard, C. (2001) Brain, 124, 941-952
[14] Hodgson, T, Mort, D, Chamberlain, M, Hutton, S, O'Neill, K. & Kennard, C. (2002) Neuropsychologia, 1413, 1-11