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pp. 1–3 (col. fig: NIL)

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44

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### What has been learned from computational models of attention

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There are few fields where neurocomputational modelling is as necessary as in that of attention - a multifaceted and 2 elusive process that is at the very core of cognition and consciousness (James, 1890). While descriptive theories of attentional functions, relying on a plethora of metaphors (spotlight/zoomlens, increased-gain, biased-competition), abound, 6 computational models that are simple enough to promote un-7 derstanding of the phenomena and make testable predictions are 8 relatively scarce. As models are often criticised for their ability to 'fit everything', imposing some degree of constraint is essen-10 tial. Neurocomputational models can answer this challenge by 11 taking on neurophysiological constraints and by addressing not 12 only behavioural but also physiological data. I start with some 13 functional considerations of the attention process, followed by 14 examples of models that help to explicate these processes and 15 some suggestions for future work. 16

The most central characteristic of attention, common to 17 all its subtypes, is a limited capacity bottleneck (Broadbent, 18 1958; James, 1890). The nature of this bottleneck, however, 19 is likely to vary with the various types. One aspect of the 20 bottleneck (the late one) involves the selection of information 21 for transfer (consolidation) to (in) short-term memory (Chun 22 & Potter, 1995; Duncan, 2006). Target selection is thought to 23 involve a type of top-down control characterised by biased-24 competition (Desimone & Duncan, 1995) and is subject to 25 capacity limitations. The bottleneck is demonstrated in multiple 26 target paradigms (Duncan, 1980), where a strong interference 27 takes place (unlike in single target with multiple distractors 28 paradigms). In the attentional blink (AB) paradigm (Raymond, 29 Shapiro, & Arnell, 1992), for example, the detection of the 30 second target (T2) is considerably depressed when it follows a 31 previous (detected) target (T1) up to intervals of about 500 ms. 32 Interestingly, when the interval between the two targets is only 33

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100 ms, the interference is minimal, posing stringent constraint 34 on computational models. Finally, a different (earlier) type of 35 bottleneck appears to be involved in bottom-up processing, 36 where visual attention seems to have the function of enhancing 37 the rate of information accrual (Smith, 2000) and of enhancing spatial resolution (Carrasco, Williams, & Yeshurun, 2002), via 39 a gain-enhancing type of mechanism. A number of models 40 addressing these processes have been developed in the last 15 41 years; due to space limitations, only a few of these important 42 models are addressed. 43

#### 1. Biased-competition

The principle of biased-competition (Desimone & Duncan, 45 1995) has been explicitly explored in a number of computa-46 tional models. Usher and Niebur (1996) have shown that a sys-47 tem using lateral inhibition between object representations can 48 make use of top-down input (or bias), corresponding to goal 49 information, in order to select a target among multiple distrac-50 tors in an effective way. The model accounts for physiological 51 data (Chelazzi, Miller, Duncan, & Desimone, 1993) and shows 52 that the selection time depends on the similarity between the 53 target and the distractors (Duncan & Humphreys, 1989). More 54 recent models have examined precise physiological measure-55 ments of attentional enhancements in V2/V4 (Deco & Rolls, 56 2005; Reynolds & Desimone, 1999). The most precise of these 57 models, recently proposed by Deco and Rolls (2005), relies on biologically realistic simulations of neural activity in the V2/V4 59 areas and demonstrates that within a very specific area of the 60 parameter-space (intra- and inter-area connectivity) one can ex-61 plain, both, the various attentional modulations and their inter-62 actions with top-down factors (contrast). The model (like that of 63 Usher and Niebur) assumes that bias is implemented via an ad-64 ditive synaptic input. This poses the problem of avoiding 'hallucinations' (responses in the absence of input), a problem which 66 can be solved with multiplicative schemes (Spratling & John-67 son, 2004). However, as demonstrated by Deco and Rolls, an 68

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2

## ARTICLE IN PRES

M. Usher / Neural Networks xx (xxxx) xxx-xxx

additive synaptic bias (complemented by the nonlinearity inherent in the neural response function) goes a large way towards 2 solving this problem, as the largest effect of the bias is at inз termediate levels of contrast (Martinez-Trujillo & Treue, 2002; 4 Reynolds & Desimone, 2003). A different type of top-down attentional control, involves control over stimulus dimensions 6 (rather than features). This type of control is exercised, both in tasks that make explicit reference to the dimensions (such as 8 Stroop) and in tasks where the dimensions are implicit (such as visual search; Weidner, Pollmann, Müller, and von Cramon (in 10 press)). Although more work is needed to explore this type of 11 control, it is remarkable that one of the earlier and most success-12 ful models of attentional control relies on additive dimensional 13 bias (Cohen, Dunbar, & McClelland, 1990). 14

#### 15 2. Attentional blink

A number of recent models have addressed the nature of 16 the capacity limitation inherent in the blink phenomena (Bat-17 tye, 2003; Bowman & Wyble, in press; Frogopanagos, Kock-18 elkoren, & Taylor, 2005; Nieuwenhuis, Gilzenrat, Holmes, & 19 Cohen, 2005). One interesting idea is that the blink reflects the 20 opening and closing of a transient attentional gate (Weichsel-21 gartner & Sperling, 1987). The nature of the gate mechanism 22 was proposed to reflect neuromodulatory responses in the Lo-23 cus Coeruleus (LC) in response to salient/target information 24 (Nieuwenhuis et al., 2005; Usher, Cohen, Servan-Schreiber, Ra-25 jkowsky, & Aston-Jones, 1999), which boosts the neural re-26 sponses and may contribute to the process of consolidation in 27 STM. Alternatively, the gate may reflect a mechanism of creat-28 ing online episodic token representations (Bowman & Wyble, 29 in press), which is distinguished from the type-representations 30 (this can help for the encoding sequences with repeated items: 31 same type but different tokens). These models account for the 32 lack of interference at 100 ms post T1 (lag-1 sparing), as a 33 result of having both targets benefiting from the attentional 34 gate (which last for about 100 ms). Moreover, the models 35 make a specific prediction: with faster presentation times (of 36 50 ms/item) the lack of interference should extend to lag-2, as 37 it falls within the gate-window (see Bowman and Wyble for experimental results confirming this prediction). Still the models 39 need to account for the virtual disappearance of the blink when 40 T1 is followed by a blank (rather than a distractor). One possi-41 bility is that targets followed by blanks trigger a stronger and 42 faster gate response, which terminates sooner (Bowman and 43 Wyble (in press); this should further predict a blink attenua-44 tion when T1 is a salient item, such as the observer's name). 45 It is unclear, however, if such a mechanism is robust enough 46 to account for the near abolishment of the blink with T1+blank 47 stimuli. Alternatively, the attention-gate may be triggered by 48 the distractor that follows T1, in order to protect it from inter-49 ference (Shapiro, Raymond, & Arnell, 1994). If the gate has a 50 width of about 100 ms, this can also explain the lag-2 sparing 51 in fast 50 ms/item sequences. This idea was implemented in an 52 interesting model, which assumes a fast system that monitors 53 conflict and modulates lateral inhibition to protect the targets 54 from interference (Battye (2003); see also, Usher and Davelaar 55

(2002) for a model where inhibition is neuromodulated to satisfy task demands). 57

#### 3. Bottom-up processing

Attention enhances visual processing even in the absence 59 of top-down (target) information. A number of models have 60 addressed this type of attentional enhancement and I will only 61 mention two approaches. The first one involves an increase in 62 the gain-function mediated by competitive interactions between 63 alternative detectors. This approach was used by Lee, Itti, Koch, 64 and Braun (1999), who demonstrated that the best account 65 for the attentional enhancement of discrimination thresholds, 66 obtains in a model where a second layer of detectors sharpens 67 the response tuning of simple responses; such sharpening can 68 be the result of a type of shunting inhibition. Increasing the 69 gain (or the lateral inhibition) can optimise choice, in situations 70 with mutually exclusive stimuli (e.g., vertical vs horizontal 71 gratings; see also Bogacz, Usher, Zhang, and McClelleland (in 72 press)). However, there are situations where such a strategy 73 will be counterproductive (when plaid stimuli have to be 74 observed). Thus, a fruitful idea for further exploration is 75 that the level of lateral inhibition is modulated to optimise 76 task demands. Attention may also enhance processing via a 77 more sophisticated mechanism than gain-enhancement, which 78 involves active recruitment of representational resources. This 79 idea is now incorporated in the various versions of the TVA 80 theory (e.g., Bundensen, Habekost, and Kyllingsbaek (2005)). 81 Finally, more work is also needed to examine the relation 82 between attentional allocation and visual grouping. Models 83 based on neural synchrony may play an important role in 84 bridging these two processes (Gross et al., 2004; Singer & Gray, 85 1995).

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58

87

# ARTICLE IN PRESS

M. Usher / Neural Networks xx (xxxx) xxx-xxx

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34

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