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Distracted and confused?: Selective attention under load

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The ability to remain focused on goal-relevant stimuli in the presence of potentially interfering distractors is crucial for any coherent cognitive function. However, simply instructing people to ignore goal-irrelevant stimuli is not sufficient for preventing their processing. Recent research reveals that distractor processing depends critically on the level and type of load involved in the processing of goal-relevant information. Whereas high perceptual load can eliminate distractor processing, high load on 'frontal' cognitive control processes increases distractor processing. These findings provide a resolution to the long-standing early and late selection debate within a load theory of attention that accommodates behavioural and neuroimaging data within a framework that integrates attention research with executive function.

Introduction

The ability to remain focused on a task is vital for any coherent cognitive function, especially when there might be potential interference from distractors that are irrelevant for the task. However, people are often distracted by task-irrelevant stimuli. Daily life provides numerous examples: a fly hovering about might distract you while reading this article, an attractive bill-board can distract a driver, and so forth. In the laboratory, research that looked at the extent to which distractor processing can be prevented led to an enduring controversy. Mixed results as to whether focusing attention on task-relevant stimuli can exclude distractors from early perceptual processing (an 'early' selection effect) or can only prevent distractors from controlling behaviour and memory (a 'late' selection effect) has fuelled a longstanding debate between early- and late-selection views of attention [1].

Recent research on the role of load in the processing of task-relevant information in determining the processing of task-irrelevant distractors offers a possible resolution. This research indicates that distractor perception can be prevented (early selection) when processing of task-relevant stimuli involves high perceptual load, and that although distractors are perceived in tasks of low perceptual load (late selection), their impact on behaviour depends on other types of load, such as that on working memory. These results have therefore provided better understanding of the circumstances under which people can achieve coherent goal-focused behavior with minimal intrusions of goal-irrelevant information.

Perceptual load studies: behavioural experiments

Research on the role of perceptual load in selective attention was triggered by the hypothesis that perception has limited capacity (as in early-selection views) but processes all stimuli in an automatic mandatory fashion (as in late-selection views) until it runs out of capacity [2,3]. This led to the predictions that high perceptual load that engages full capacity in relevant processing would leave no spare capacity for perception of task-irrelevant stimuli. In situations of low perceptual load, however, any capacity not taken up in perception of task-relevant stimuli would involuntarily 'spill over' to the perception of task-irrelevant distractors. These predictions were tested in experiments that assessed the effects on distractor perception of varying perceptual load in the task-relevant processing [3–5].

Increased perceptual load means that either the number of different-identity items that need to be perceived is increased, or that for the same number of items perceptual identification is more demanding on attention [3–5] (see Figure 1). These experiments found that increased perceptual load reduces, indeed typically eliminates, any distractor interference effects, in support of the perceptual load hypothesis.

Reduced distractor interference under conditions of high perceptual load is not simply the result of the general increase in task difficulty with load and the associated slowing of performance. Manipulations of extreme sensory degradation (e.g. reducing the target size or contrast so much so that it is barely seen) that cannot be compensated for by applying more attention – in other words subjecting target identification to sensory 'data limits' rather than attentional 'resource limits' [6] – increase the general task difficulty (i.e. reduce speed and accuracy, compared with an intact target) but do not reduce distractor interference [7]. Alternative accounts to perceptual load in terms of general task difficulty or slowing are also ruled out by the findings (reviewed later) that increasing load on cognitive control processes (e.g. working memory) increases task difficulty but has the opposite effect to perceptual load, resulting in an increase (rather than a decrease) in distractor interference.

The studies mentioned so far assessed perception of the distractor identity in the 'response competition' paradigm (Figure 1). Other paradigms used since have included

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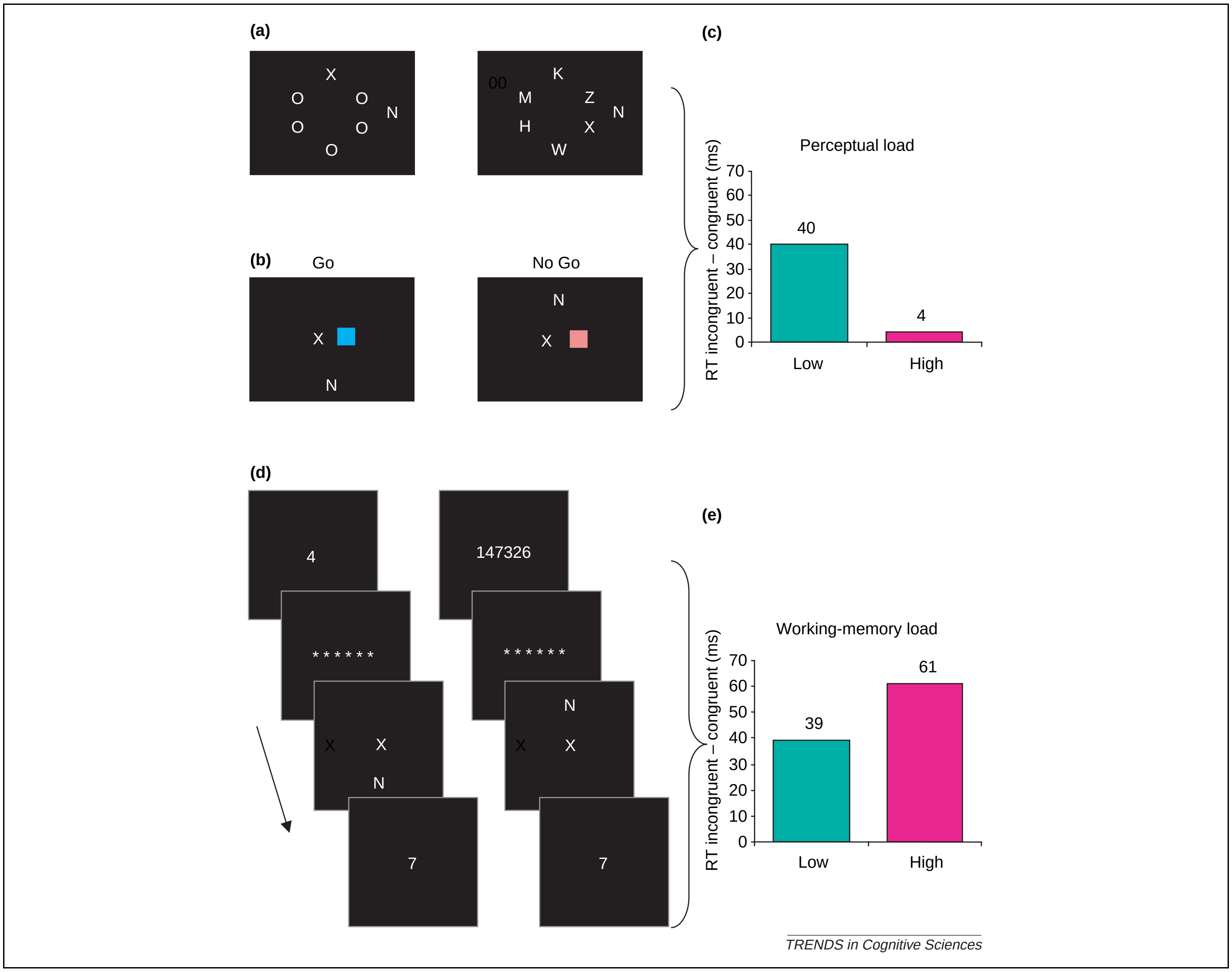

Figure 1. Examples of stimuli and results in behavioural load experiments, using the response-competition paradigm. **(a–c)** Subjects make speeded responses indicating whether a central target letter is one of two pre-specified letters (X or N) while attempting to ignore a peripheral distractor letter. Slower responses in the presence of an incongruent distractor (shown in a) compared with a congruent distractor (e.g. X distractor for X target) indicate that the distractor identity was perceived. **(a)** Perceptual load is manipulated by varying the number of items (letters) that are similar to the target (no similar items in low load, left; five in high load, right) [4]. Other experiments [3,5] varied the number of task-relevant items by presenting the target letter with fewer (up to three) non-target letters of different identities in conditions of low perceptual load. **(b)** Perceptual load is manipulated by increasing perceptual processing requirements for the same displays. Whether target letter responses are made (Go trials) or not (No-Go trials) depends either on detecting the presence of any blue shape (low load), or on discrimination of conjunctions of colour and shape (high load; e.g. target responses are made only if there is a blue square and a red circle). See [51] for review of previous evidence that feature versus conjunction tasks impose low and high load, respectively, on attention. **(c)** Distractor effects are greater in low than in high perceptual load conditions. **(d)** Working-memory load is manipulated during performance of a response-competition task. Subjects are required to memorize the set of either one (low load) or six (high load) digits presented at the start of each trial, to indicate whether a memory probe digit presented at the end of each trial was present or absent in the set. **(e)** Working-memory load has the opposite effect on distractor processing to perceptual load: distractor effects are greater in high than in low working-memory load.

measures of implicit learning about spatial configuration of irrelevant distractors [8], as well as measures of both positive priming (Thoma and Lavie, unpublished), and negative priming effects from distractors that are presented as targets on subsequent trials [9]. All these different approaches have converged in showing that distractor effects are eliminated under high perceptual load in target processing (but see Box 1 for some exceptional distractors). This generalization of perceptual-load effects across multiple measures of distractor processing provides support for the suggestion that distractors are simply not perceived when the perception of task-relevant stimuli under high load consumes all or most of the available capacity. Neuroimaging studies also indicate this, as reviewed next.

Effects of perceptual load on distractor processing in the brain

Several neuroimaging studies show that high perceptual load in a relevant task modulates neural activity related to irrelevant distractors. In one study [10] neural activity in visual cortex associated with the perception of irrelevant motion distractors was determined by the level of load in a relevant task performed on words at fixation. Subjects were asked either to monitor a word's case (low load) or number of syllables (high load). Irrelevant motion background evoked responses in motion selective cortices (e.g. MT, V1/V2) in low-load but not high-load conditions. In another study [11], activations related to written words were not elicited when subjects ignored them while performing a high-load task of monitoring a rapid

Box 1. Exceptional distractor stimuli: interference by famous distractor faces

Lavie *et al.* [38] found that interference by meaningful 3D distractor pictures on a name-categorization task (e.g. fruits versus musical instruments; Fig. Ia) depends on the level of perceptual load (number of letter-strings) in the task. By contrast, interference by famous distractor faces is unaffected by the level of perceptual load (again, number of letter-strings) in a famous-name categorization task (pop stars versus statesmen; Fig. Ib). Famous but task-irrelevant distractor faces were also found to produce long-term covert priming effects (speeding up familiarity decisions following their pre-exposure) regardless of the level of relevant task load during first exposure [39]. Thus, it seems that people are more susceptible to interference by distractor stimuli of social significance, such as famous faces. These produce interference and priming effects regardless of whether attention is fully engaged in a task of high perceptual load.

By contrast, long-term explicit recognition memory of any distractor faces presented in the experiment, either famous or anonymous, does depend on the level of load in the relevant task and is, in fact, no better than chance in tasks of high load (search for a target letter among similar non-target letters) [39,40]. The finding that explicit long-term memory depends on load is consistent with the established finding that long-term memory depends on depth of encoding. A more shallow encoding resulting from attentional engagement in a high-load task might be sufficient to produce priming and RT interference effects but not explicit long-term recognition. The dependence of recognition memory for task-irrelevant stimuli on the level of load in a relevant task may have practical implications. For example, eyewitness testimony will often be based on explicit recognition of faces that were encountered while the observer was engaged in some other attention-demanding task.

Fig. I. Examples of displays used in Lavie *et al.* [38]. **(a)** An example of a high-load display in the object name-categorization task with an incongruent distractor object. **(b)** An example of a high load display in the face name-categorization task with an incongruent distractor face. In the low-load conditions the target name had to be searched among a smaller number of letter strings. Reproduced with permission from [38].

superimposed picture stream for repetitions. Similarly, when subjects attempt to ignore pictures of places presented in the background while monitoring for face repetitions at the fixation point, parahippocampal activity related to the place backgrounds is substantially reduced by increasing the load in the face identification task (by adding noise to each face) [12]. Moreover, repetition of some of the backgrounds leads to attenuation of the stimulus-specific fMRI signal (fMR adaptation or 'repetition suppression' [13]) only when the face task is carried under low load; this effect is abolished with high perceptual load. This result has a striking implication, namely, that the brain does not discriminate between novel and repeated backgrounds when attention is fully engaged in a high-load task. Modulation of activity related to task-irrelevant stimuli in the ventral stream can be long-ranging: activity related to colourful pictures presented to one hemifield in V4 is modulated by load in a task performed on pictures in the other hemifield [14]. Moreover the reduction of distractor-related-activity by increasing load was accompanied by enhancement of target-related activity in this study, providing evidence for long-ranging, capacity-limited 'push–pull' effects of selective attention in V4 [14].

Thus, it seems that engaging attention in processing task-relevant stimuli with high perceptual load substantially reduces and can even eliminate any neural signal detected with fMRI related to potent distractor stimuli, such as meaningful words, places and motion, as well as differential neural activity for novel versus repeated backgrounds. Even the differential amygdala response to emotional face expressions (e.g. happy, angry or fearful) compared with neutral faces that is found when subjects attend to the faces and even under some conditions of apparent inattention [15], is abolished when subjects ignore the faces while performing a high-load task (requiring subtle orientation discriminations) [16]. Such findings challenge claims that amygdala function and emotional effects always bypass attention [15]. Instead they suggest that the task-relevant processing in the studies that led to those claims was not sufficiently loaded to prevent attention spilling over to the emotional distractors.

How early is the gating of neural processing by load?

Effects of perceptual load in a relevant task can be found in V1 activity related to irrelevant stimuli. Schwartz *et al.* [17] assessed activity related to peripheral task-irrelevant checkerboard patterns presented while subjects performed a task of either low or high load on a rapid letter stream at fixation (Figure 2a). They found that visual cortex activity related to the task-irrelevant checkerboard was decreased by higher load in the central task. Importantly, retinotopic mapping revealed activation in areas V1, V2 and V3 as well as ventral V4 in each subject. This analysis showed that the decrease in neural response to peripheral checkerboards by higher central load was clearly found in V1, although effects of load became larger for successive extrastriate areas through to V4 (Figure 2b).

Another study [18] similarly found that visual cortex activity related to peripheral checkerboards was significantly reduced by performance of a high-load task at fixation (monitoring for letters among similar characters in a rapid stream) compared with a low-load task (monitoring a colour change). Retinotopic mapping again showed that the effects occurred throughout visual cortex, increasing in magnitude from V1 through to V4. An important finding in this study was that activity related to the irrelevant checkerboards in the Lateral Geniculate Nucleus (LGN), the major thalamic component in the

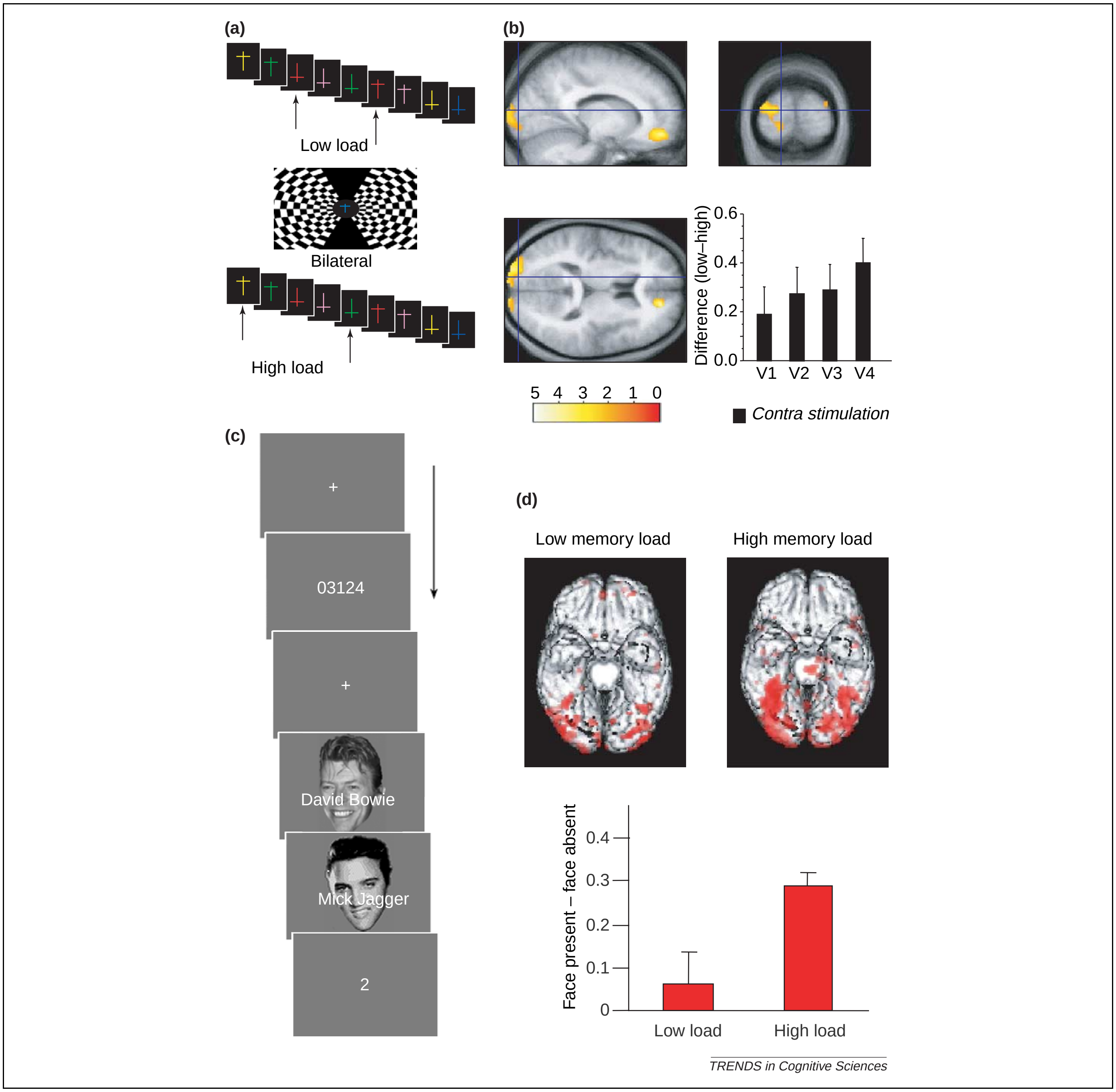

Figure 2. Examples of stimuli and results in imaging load studies. **(a)** Stimuli and procedure used in a perceptual load imaging experiment [17]. A rapid stream of coloured stimuli was presented at fixation with flickering checkerboards presented on the left or right, both sides (shown) or neither side. In the low-load task participants had to detect any red shape; in the high-load task, they had to detect specific conjunctions of colour and shape (e.g. yellow upright or green inverted crosses). Note that although the conjunction task loads both perception and visual short-term memory it should not load the executive control processes involved in distractor rejection (discussed in the last section of this article). Reproduced with permission from [17]. **(b)** Visual cortex activity related to the checkerboards (pooled across unilateral and bilateral conditions) is greater in the low-load than in the high-load tasks, as shown in mid-saggital, coronal and transverse sections. The bar graph shows that this difference increases across visual areas V1–V4. **(c)** Examples of stimuli and procedure used in a working-memory load imaging experiment [33]. Subjects had to memorize a set of digits in a random order (high load, shown) or in a fixed order ('01234', low load) presented at the start of each trial, and press a key to indicate which digit in the memory set followed the memory probe digit presented at the end of each trial (the correct reply in this example is 4). During the memorizing task subjects also have to perform a Stroop-like task, classifying names into politicians and pop-stars while attempting to ignore distractor faces that are either congruent or incongruent with the name. **(d)** Visual cortex activity related to the presence of the face is greater in the high-load than in the low-load tasks. (c,d) Reproduced with permission from [33].

retinocortical projection, was also modulated by load (but see also [17]). The LGN is often viewed as the gateway for entry of sensory information into visual cortex and represents the first stage at which cortical top-down signals could affect visual processing. Perceptual load can therefore affect even the earliest processing site in the visual pathway.

The suggestion that high load in a central task gates processing of irrelevant stimuli in visual cortex is in line with the effects of load on early evoked event-related potentials (ERPs) to irrelevant stimuli arising from visual cortex. Measures of the sensory ERPs to distractor and target under conditions of low load (simple feature detection) or high load (harder letter discrimination)

Box 2. Age-related changes in capacity and distraction: interaction of age and load effects

Theories about age-related changes to cognition generally hold that effortful cognitive abilities that consolidate relatively late in development are the first to weaken in old age. It has also been specifically suggested that information-processing capacity develops throughout childhood but regresses in later life. Therefore, by comparison with mature (young to middle-aged) adults, younger children and older adults should have smaller information processing capacity. This proposal, when taken together with the perceptual-load model leads to a somewhat counterintuitive prediction that distractor interference would be prevented by lower levels of relevant-task load in younger children and older adults as these would be sufficient to exhaust their more limited capacity by comparison with mature adults. This prediction was in fact supported in two studies. One study showed that smaller increases in the number of relevant-search items were needed to reduce distractor interference in the elderly [41] (Fig. I), and another found the same pattern for younger school-age children [42]. Both studies also found that the older and younger subjects suffered from greater distractor interference under very low levels of load (Fig. I), highlighting an additional age-related change in the ability to control interference by irrelevant stimuli when these are perceived. These studies therefore demonstrate that the deficits in cognitive control against distractor interference in children and elderly can be ameliorated by small increases in the level of perceptual load in the task relevant stimuli.

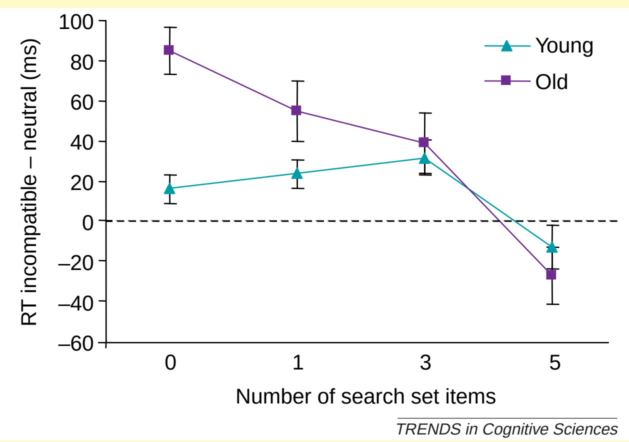

Fig. I. The effects of perceptual load on distractor response-competition effects in young (cyan) and old (purple) age groups [41]. Shown are the distractor effects (mean RT differences ± standard error between the incompatible and neutral conditions) as a function of the number of search items in a central search task and age group. The same effects are found when general slowing of RT with age is taken into account by calculating the distractor effects as proportions of the baseline RTs. Reproduced with permission from [41].

show that the amplitude of the occipital (P1) potential at 80–130 ms after distractor presentation is significantly reduced by perceptual load [19].

Perceptual load and spatial attention

The effects of perceptual load require clear spatial separation between the target and distractor. When both target and distractor are parts of the same stimulus (e.g. a coloured word in the Stroop task [20]) high perceptual load (manipulated similarly to Figure 1b) can increase rather than decrease Stroop interference [21]. It is likely that when the distractor and target form parts of the same stimulus, paying more attention to the target (under high perceptual load) results in more attention to the distractor as well.

Indeed, in conditions where there is a spatial separation of target and distractor, reduced distractor processing in high perceptual load might be due to narrowing of a spatial attention window around the target space, effectively excluding stimuli outside it. In support of this suggestion, spatial cueing effects on target RTs [22] and on the amplitude of both occipital P1 and N1 ERPs [23] are stronger with high than with low load on target perception. Although there are some reports of diminished distractor effects with target cueing under conditions of low load [22,24], it remains unclear whether these results show that attention can narrow its focus to encompass just the target region even under low load, or are due instead to eye-movements to the target and away from the distractor (which were likely to occur in the long durations used).

Crossmodal effects of perceptual load

It is important to determine whether attentional capacity is modality specific (such that, for example, auditory load should have no effects on the perception of visual distractors) or is shared between the modalities (such that load in one modality should determine distractor processing in another modality). With the prevailing emphasis in the last few decades on attention in vision, most load studies to date have been conducted in the visual modality, although a few studies have now examined crossmodal load effects.

One study replicated the within-modality visual load effects on distractor processing reported earlier by Lavie and Cox [4], but found that auditory presentation of the distractor letters resulted in greater distractor effects with high (versus low) load in the visual search task [25]. However, as the auditory distractors had their offset 200 ms later than the visual display, it seems likely that there was more of a temporal overlap in visual target and auditory distractor processing in the high-load conditions (in which the target was likely to be processed later) than in the low-load conditions. Further work that considers the time course of crossmodal response-competition effects is needed on this.

A few studies have now examined whether processing visual distractors depends on load in an auditory task. Although they all used a modification of the task used by Rees *et al.* [10] the results have been rather mixed. In their later study, Rees *et al.* [26] required subjects to ignore visual motion while monitoring an auditory word stream either for words spoken in a louder voice (low load), or for number of syllables (high load) during scanning. They found that neural activity related to irrelevant visual motion was unaffected by auditory load. Moreover, prolonged exposure to motion produces a motion after-effect (MAE), whereby a subsequently static stimulus appears to move in the opposite direction to the one adapted during pre-exposure. A direct comparison of the effects of load between visual and auditory tasks on subsequent subjective durations of the MAE revealed that compared with low load, high visual load reduced the subjective durations of MAE, but these were unchanged by high auditory load.

By contrast, another study [27] found that fMRI activity related to irrelevant motion (e.g. activity in MT)

Box 3. Plasticity related changes in the effects of load

The effects of plasticity on information-processing capacity can be clarified by considering their sensitivity to load manipulations. In the case of congenital deafness, there have been mixed results regarding the question of whether deafness leads to a general improvement in visual performance (perhaps reflecting compensation for the loss of hearing by enhancement of vision) [43], to improvement only in peripheral vision [44,45] or no improvement at all [46]. Manipulation of perceptual load for a task in the parafovea (similar to that used in Figure 1a in main text, but with shapes instead of letters) while presenting distractors either at fixation or at the periphery, showed that a greater increase in the task load was needed to reduce interference by an irrelevant peripheral distractor in deaf than in hearing individuals. However, smaller increases in load were needed to reduce interference by a fixated distractor in deaf than in hearing individuals [47]. These findings are best accounted for by suggesting that congenital deafness does not lead to any increase in visual capacity (not even just in peripheral vision) but instead leads to a shift in the spatial distribution of capacity from the centre of the visual field to the periphery. Such a shift could serve a compensatory role in the absence of orienting to the far periphery via hearing.

Another case of changes in information-processing capacity due to plasticity is that of experience with video-game playing. In contrast to the typical reduction in distractor processing with load, manipulations of load in visual search tasks had no effects on processing task-irrelevant distractors in expert video game players [48]. Further findings of superior performance by video game players in other measures of capacity (e.g. the number of items that can be subitized, visual detection abilities) confirm that expert game players have enhanced visual information-processing capacity rather than greater distractibility. Similar effects following specific training in video-game playing in non-expert players confirm a causal effect of video-game playing on attentional capacity.

as well as the MAE were reduced by high load in a letter monitoring task (monitor for vowels) compared with passive fixation, both for visual or auditory letter presentations. MAE modulation by an auditory task of high load (monitoring an auditory digit stream for repetitions of odd numbers) compared with passive fixation was also replicated in another study [28].

This apparent conflict might be resolved by pointing to procedural differences between the studies. Rees *et al.* [26] monitored eye movements and compared motion processing between two levels of load. By contrast, the two studies that found reduced motion processing with auditory load [27,28] did not monitor eye movements and compared motion processing between performance of a high-load task and passive fixation. It is therefore possible that eye movements (away from the motion stimulus) under high auditory load as well as any other differences of passive fixation and task performance (e.g. demands on response selection) are responsible for the reduction in motion processing by auditory load.

Improving distractor rejection in neuropsychological patients with perceptual load

Improvement in distractor rejection with a small increase in load is found for patients with a lesion to brain regions that are thought to mediate attentional capacities (see Box 2 for similar improvements in children and the elderly). Left neglect patients with a right parietal lesion are particularly distracted by stimuli in their right field. However, only a small increase of perceptual load in the task performed at fixation (increasing the number of letters in a search task from one to two) is sufficient to reduce interference by a right distractor in these patients (but not in non-brain-damaged controls who need a larger increase in load) [29]. Similarly, a patient with a bilateral lesion of frontal and temporal areas showed greater interference than non-brain-damaged controls from both right and left distractor words, but these distractor interference effects were substantially reduced with a small increase in load (the addition of just one letter string to the display), an effect not found in the controls [30]. These findings suggest that although the lesions in these patients involved a general reduction in attentional capacity [31] – because small increases in task load that had no effect on the control group exhausted the patients' capacity – these capacity limits can be used beneficially to improve distractor rejection with small increases in the task load (see Box 3 for load studies on populations that appear to have increased visual capacity).

Loading cognitive control processes

The effects of load on distractor processing depend crucially on the type of mental processing that is loaded. Load on executive cognitive control functions, such as working memory, that renders them unavailable to actively maintain stimulus-processing priorities throughout task performance has the opposite effect to perceptual load: it increases interference by irrelevant low-priority distractors rather than decreases it. Behavioural studies demonstrate that high working-memory load can increase distractor response-competition effects on behaviour [5,32] (Figure 1d,e) and neuroimaging studies show that visual cortex activity related to the presence of distractors (faces) can also be increased by high working-memory load [33] (Figure 2c,d). Attentional capture by a salient but task-irrelevant odd colour 'singleton' distractor, during shape-based search tasks, is also increased by high working-memory load [34,35]. By contrast, loading working memory with task-unrelated material does not reduce search efficiency in the absence of a singleton distractor [36,37], and does not enhance neural responses to ignored place images presented in the background [12]. This contrast between the significant effects of working-memory load on interference by potent (response-incongruent or salient singleton) distractors [5,32–35] and the failures to find such effects on rejection of ordinary search non-targets or background pictures [12,36,37] suggests that active cognitive control of visual selective attention may only be needed to resolve conflict between targets and a potent salient distractor that strongly competes with the target.

The accommodation of the effects of different types of load on distractor processing within the same load model [5,32] rules out alternative accounts for either type of load effect in terms of general task difficulty alone, and provides a better understanding of how distractor processing is affected by capacity limits in different mental processes. Such a load model also provides a more complete resolution for the early- and late-selection debate: early selection critically depends on high perceptual load and cannot be achieved simply by exerting active cognitive control. Successful late selection, however, (namely, correct target responses despite perception of potent but irrelevant distractors, as in situations of low perceptual load) critically depends on active cognitive control functions being available for the selective attention task.

Conclusions

The studies reviewed here illustrate the importance of considering the level and type of load involved in the task performed to determine interference by task-irrelevant distractors. Simply instructing people to focus attention on a certain task is not sufficient to prevent distractor interference. A high perceptual load that engages full attention in the task is also needed. In contrast with the effects of perceptual load, high cognitive-control load increases distractor interference, suggesting that cognitive control is needed for actively maintaining the distinction between targets and distractors. These findings resolve the long-standing early- versus late-selection debate and also clarify the role of cognitive control in visual selective attention. Future research should aim to provide an explicit neural model that can accommodate the numerous demonstrations that distractor-related neural activity is determined by the level and type of load in task-relevant processing. Although this conclusion was predicted from the psychological account, the source for limited capacity at the neural level and the exact mechanism by which neural capacity limits determine distractor processing in the brain remain to be clarified, but there are several promising avenues for further explorations (see Box 4).

Box 4. Questions for future research

- One suggestion for the neural basis of capacity limits proposes that receptive fields are the limited-capacity neural resource for which stimuli compete [49]. Whether this can explain perceptual-load effects on distractor-related neural activity can be tested by asking whether perceptual load will only affect representations that share receptive fields but not representations in separate fields.
- The findings that famous distractor faces are processed at some level regardless of the level of perceptual load task-relevant processing [38,39] can be accounted for in terms of attentional priority for stimuli of high social significance (see Box 1). However, this appears to be at odds with the findings that differential amygdala responses to emotional facial expressions (which are presumably also of high social significance) can be abolished by high perceptual load [16]. Methodological differences between the studies preclude a conclusive answer. Future studies should determine whether the effects of load on perception of emotional faces and famous faces are still different when the same measures are used.
- With the exception of famous faces and emotional faces, most load effects to date were established using fairly neutral distractor stimuli. It should be interesting to ask whether the processing of other meaningful stimuli is also determined by load, for example, social interaction cues or biological motion.
- The findings that small increases in perceptual load in a relevant task can improve distractor rejection in the young and elderly (Box 2), as well as in neuropsychological patients, raise the possibility that other populations that are prone to distraction could also benefit from such load manipulations (e.g. schizophrenic patients, children characterized with ADHD).
- Load effects have been established in humans, but a report on perceptual-load effects on the ability of birds to detect predator-like stimuli [50] raises the possibility that the principle reflected in load effects is general to all biological information-processing systems. It would be interesting to examine whether load effects on detection of task-irrelevant stimuli can be found in a variety of species, both primates and non-primates.

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