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Authors

Wiech, Katja
Vandekerckhove, Joachim
Zaman, Jonas
[et al.](#)

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were allowed to view our horse stimuli at close range they showed similar reactions to all three conditions (all cues visible, eyes covered, ears covered), which were significantly different from their responses to appropriately matched control stimuli (phase-scrambled counterparts of the originals; Supplemental Information). Furthermore, subjects were more likely to approach the original stimuli and more likely to avoid the controls, as would be predicted if they were responding to photographs of horses versus novel objects (see details in Supplemental Information). We also took precautions to avoid the possibility of a 'Clever Hans Effect' occurring through incidental cueing by the experimenter. In particular, the experimenter was unfamiliar to the horse, kept ignorant of which stimuli would be presented and, crucially, after the release point (when the choice was made) they stood facing away from the horse, so could not see the horse's choice or provide any feedback (full details in Supplemental Information).

Our results provide the first evidence from an animal with laterally placed eyes that cues from this area convey important information. Eye gaze is difficult to isolate in animals with eyes positioned at an oblique angle, and it had been suggested that non-primates cannot use eye gaze independently of head orientation [2,4]. However, we demonstrate that the eyes do carry information, even when laterally placed in an animal far removed from the primate lineage. Horses, along with other ungulates, have a white sclera that is visible in various situations [6]. This plus other cues, such as dilation of the pupil and movement of the facial muscles surrounding the eye, could be informative of attentional state, as they are in humans [8].

Most significantly, our results demonstrate that animals with large, mobile ears can use these as a visual cue to attention. While anecdotal accounts of this exist in the literature (for example [6]) the potential role of the ears in signaling has been overlooked in previous experiments. In animals that have evolved a differently shaped face it is important to consider cues that humans do not have, and novel paradigms that incorporate these will be crucial in developing a full understanding of attentional mechanisms across species.

Supplemental Information

Supplemental Information includes experimental procedures, supplemental results, one figure, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.06.023>.

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Mammal Vocal Communication and Cognition Research, School of Psychology, University of Sussex, Brighton, BN1 9QH, UK.
E-mail: j.wathan@sussex.ac.uk,
karenm@sussex.ac.uk

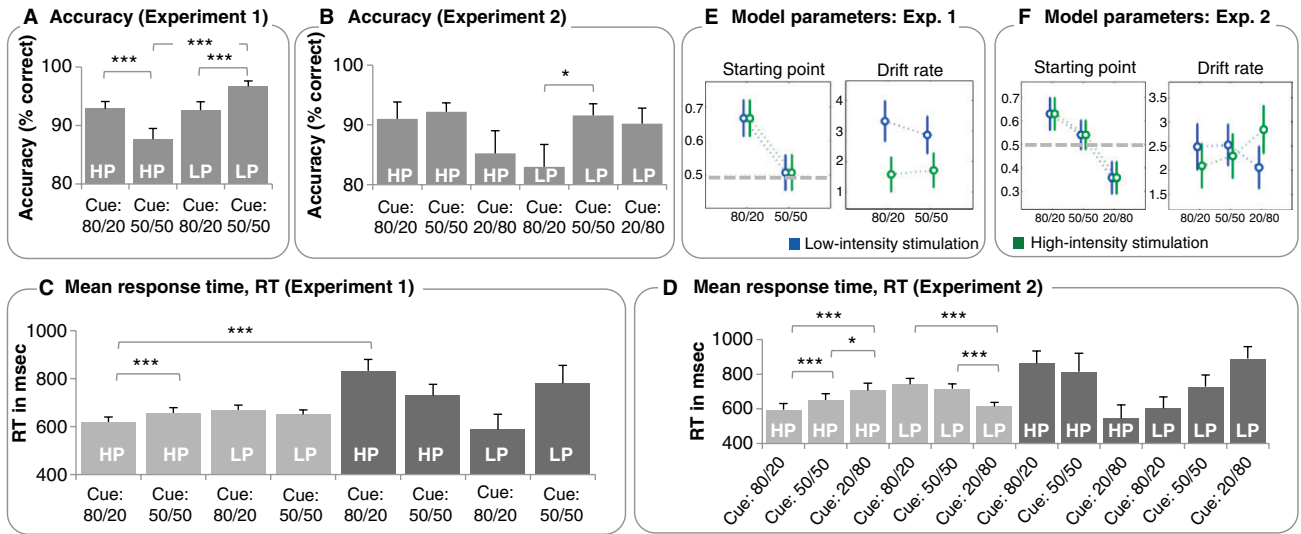
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Influence of prior information on pain involves biased perceptual decision-making

Katja Wiech^{1,2,*},
Joachim Vandekerckhove^{3,4},
Jonas Zaman⁴, Francis Tuerlinckx⁴,
Johan W.S. Vlaeyen^{4,5},
and Irene Tracey^{1,2}

Prior information about features of a stimulus is a strong modulator of perception. For instance, the prospect of more intense pain leads to an increased perception of pain, whereas the expectation of analgesia reduces pain, as shown in placebo analgesia and expectancy modulations during drug administration [1]. This influence is commonly assumed to be rooted in altered sensory processing and expectancy-related modulations in the spinal cord [2], are often taken as evidence for this notion. Contemporary models of perception, however, suggest that prior information can also modulate perception by biasing perceptual decision-making — the inferential process underlying perception in which prior information is used to interpret sensory information. In this type of bias, the information is already present in the system before the stimulus is observed [3]. Computational models can distinguish between changes in sensory processing and altered decision-making as they result in different response times for incorrect choices in a perceptual decision-making task (Figure S1A,B) [4]. Using a drift-diffusion model, we investigated the influence of both processes in two independent experiments. The results of both experiments strongly suggest that these changes in pain perception are predominantly based on altered perceptual decision-making.

Thirty-four right-handed healthy volunteers (23 female; mean age 23.4 years) took part in the study in Experiment 1. In a probabilistic cueing paradigm, participants were presented with one of two visual cues in each trial. Cue 1 signaled the subsequent application of a high intensity noxious electrical stimulus with a probability of 80% and of a low intensity stimulus with a probability of 20%. Cue 2



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Figure 1. Biased sensory processing or altered perceptual decision-making?

Mean decision accuracies for the four experimental conditions in Experiment 1 (A) and the six conditions in Experiment 2 (B) (HP, high intensity pain; LP, low intensity pain). (C,D) Mean response times for correct responses (light grey) and incorrect responses (dark grey; HP, high intensity pain; LP, low intensity pain). (E,F) The group average of the modelling parameters starting point (left) and drift rate (right) in Experiment 1 (E) and Experiment 2 (F). The dashed line indicates a neutral starting point of 0.5 for reference.

signaled an equal probability (i.e. 50%) for both high and low intensity stimuli. To test whether the results of Experiment 1 were specific for prior information about high intensity pain, we conducted a second experiment (N = 22; 11 female; mean age 26 years) with an additional condition in which a third cue signaled a prior probability of 20% for high intensity pain and an 80% probability for low intensity pain.

In both experiments, participants had to indicate as quickly as possible upon stimulus delivery whether they had received a low-intensity or high-intensity stimulation. Decision accuracy and response time were recorded as outcome parameters (Figure 1A–D). Using a hierarchical diffusion model [5], we compared the influence of the cues on drift rate (indicative of altered sensory processing) and on the starting point of the decision-making process (indicative of altered perceptual decision-making) by fitting a model that allowed for an influence of cue information on drift rate and starting point. Further free parameters of the model were non-decision time and boundary separation (see Supplemental Information for details). For each of the four parameters, Bayesian paired contrast tests were applied to test for effects of cue condition (Experiment 1: ‘80/20’, ‘50/50’; Experiment 2: ‘80/20’, ‘20/80’ or ‘50/50’) and

stimulation intensity (i.e. high or low) and their interactions.

In both experiments, only the starting point showed a main effect of cue (for details see Supplemental Information), indicating that prior information biases perceptual decision-making (Figure 1E,F). In Experiment 1, participants showed a shift in starting point towards high intensity pain in the ‘80/20’ condition. In Experiment 2, the starting point was shifted towards high pain in the ‘80/20’ condition and towards low pain in the ‘20/80’ condition. The degree of shift in starting point away from the neutral starting point did not differ between the two conditions.

Both datasets also showed changes in drift rate (indicating altered sensory processing), which were, however, more closely related to the stimulation intensity than the cue condition. In Experiment 1, low-intensity stimuli yielded higher drift rates than high-intensity stimuli, irrespective of the cue condition. In Experiment 2, the drift rate in the ‘20/80’ condition was significantly increased if high-intensity stimuli were applied, indicating a ‘pop-out’ effect of unexpectedly high stimuli. None of the remaining comparisons, including those for non-decision time or boundary separation, reached significance.

The observation that prior information affects the perception

of pain is not novel. There is ample evidence showing that pain can be amplified through negative expectations and reduced through expectations of pain relief [6]. However, neural mechanisms underlying these changes are still unclear. A prevalent explanation based on related studies using expectancy manipulations assumes that prior information changes the signal level in brain regions involved in processing sensory-discriminative aspects of pain. However, changes in pain perception can also be reflected in brain regions related to cognitive-affective processing [7]. Activation changes in sensory-discriminative brain regions are nevertheless considered the gold standard when proving genuine changes in pain perception as opposed to report bias.

Our data suggest that cognitive pain modulation can also be rooted in altered perceptual decision-making. Over recent years, the conceptualization of perception as an inferential process has critically changed our understanding of perception–cognition interactions. The basic tenet of this account is that incoming sensory information is not analyzed *de novo* but interpreted based on prior information. As a consequence, incoming information is more likely to be interpreted in accordance with the

more likely percept. To date, the effect of prior information on perceptual decisions has mainly been studied in basic visual processing [8–10]. Our data critically extend these findings by showing that biased perceptual decision-making is pivotal to the modulation of pain, one of the most common and costly health care problems worldwide.

Our findings have several far-reaching implications. First, they challenge the current emphasis of neuroimaging studies investigating cognitive pain modulation on the search for changes in brain regions related to sensory-discriminative processing as too narrow. Research outside the pain domain has linked altered perceptual decision-making to activation changes in the anterior cingulate cortex (ACC) and the dorsolateral prefrontal cortex (DLPFC) [8], which have also been implicated in cognitive pain modulation [7]. Future studies have to identify neural processes underlying biased perceptual decision-making and probe their utility as objective indicators of pain modulation. Note that a bias in perceptual decision-making as observed here is not to be equated with report bias in which the report is decoupled from the perceptual process. Second, future studies have to specify the relative influence of processes such as expectations, attention, uncertainty and feedback-driven learning that may underlie or mediate the effects of prior probability information and the generalisability of our findings for other types of peripheral input and perceptual experiences. Finally, it needs to be explored how our findings relate to previous studies in which the same stimulation intensity and probability was used in all conditions [1,2]. Modern conceptions of perception have begun to embrace evidence on cognitive influences onto perception. Our data strongly encourage this perspective to allow for a more comprehensive view on perception in general and clinical challenges such as pain in particular.

Supplemental Information

Supplemental Information includes a detailed description of the results, experimental procedures, two tables, references and the full definition of the hierarchical diffusion model and can be found with this article online at [10.1016/j.cub.2014.06.022](https://doi.org/10.1016/j.cub.2014.06.022).

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¹Oxford Centre for Functional Magnetic Resonance Imaging of the Brain and ²Nuffield Dept. of Clinical Neurosciences, Univ. of Oxford, JR Hospital, Oxford OX3 9DU, UK.

³Dept. of Cognitive Sciences, 2324 SBSG, UC Irvine, CA 92697-5100, USA. ⁴Faculty of Psychology and Educational Sciences, Univ. of Leuven, Tiensestraat 102, 3000 Leuven, Belgium. ⁵Dept. Clinical Psychological Science, Maastricht University, P.O. Box 616, 6200 MD Maastricht, Netherlands.

*E-mail: katja.wiech@ndcn.ox.ac.uk

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A strong link between speed of visual discrimination and cognitive ageing

Stuart J. Ritchie^{1,2,*},
Elliot M. Tucker-Drob³,
and Ian J. Deary^{1,2}

Attempts to explain people's differences in intelligence and cognitive ageing often hypothesize that they are founded substantially upon differences in speed of information processing [1]. To date, there are no studies that fulfill the design criteria necessary to test this idea, namely: having a large sample size; being sufficiently longitudinal; and using measures of processing efficiency that have a tractable biological basis, are grounded in theory, and are not themselves complex or based on motor response speed. We measured visual 'inspection time', a psychophysical indicator of the efficiency of the early stages of perceptual processing [2], in a large ($n = 628$ with full data), narrow-age sample at mean ages 70, 73, and 76 years. We included concurrent tests of intelligence. A latent growth curve model assessed the extent to which inspection time change is coupled with change in intelligence. Results showed a moderate correlation ($r = 0.460$) between inspection time performance and intelligence, and a strong correlation between change in inspection time and change in intelligence from 70 to 76 ($r = 0.779$). These results support the processing speed theory of cognitive ageing. They go beyond cross-sectional correlation to show that cognitive change is accompanied by changes in basic visual information processing as we age.

The processing speed theory of cognitive ageing posits that a decline in the efficiency with which simple mental operations can be correctly completed is fundamental to ageing-related declines in higher cognitive functions [1]. Many studies have modeled the correlations of so-called processing speed measures with cognitive abilities such as spatial skill [3]. Typical studies use tests such as