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Expectancy modulates pupil size during endogenous orienting of spatial attention

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ABSTRACT

fMRI investigations in healthy humans have documented phasic changes in the level of activation of the right temporal-parietal junction (TPJ) during cued voluntary orienting of spatial attention. Cues that correctly predict the position of upcoming targets in the majority of trials, i.e., predictive cues, produce higher deactivation of the right TPJ as compared with non-predictive cues. Since the right TPJ is the recipient of noradrenergic (NE) innervation, it has been hypothesised that changes in the level of TPJ activity are matched with changes in the level of NE activity. Based on aforementioned fMRI findings, this might imply that orienting with predictive cues is matched with different levels of NE activity as compared with non-predictive cues. To test this hypothesis, we measured changes in pupil dilation, an indirect index of NE activity, during voluntary orienting of attention with highly predictive (80% validity) or non-predictive (50% validity) cues. In agreement with current interpretations of the tonic/phasic activity of the Locus Coeruleus-Norepinephrinic system (LC-NE), we found that the steady level of cue predictiveness that characterised both the predictive and non-predictive conditions caused, across consecutive blocks of trials, a progressive decrement in pupil dilation during the baseline-fixation period that anticipated the cue period. With predictive cues we observed increased pupil dilation as compared with non-predictive cues. In addition, the relative reduction in pupil size observed with non-predictive cues increased as a function of cue-duration. These results show that changes in the predictiveness of cues that guide voluntary orienting of spatial attention are matched with changes in pupil dilation and, putatively, with corresponding changes in LC-NE activity.

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1. Introduction

To cope with capacity limits in the processing of incoming sensory inputs, the brain orients attention toward relevant stimulus features or locations and filters out irrelevant ones (Petersen & Posner, 2012). fMRI investigations in healthy humans have demonstrated that during voluntary orienting of attention, expectancy about the occurrence of attentional targets modulates the level of BOLD activation in the temporal parietal junction (TPJ) and the filtering out of distracting non-target items and non-target positions. Two different types of modulation have been observed. Shulman, Astafiev, McAvoy, d'Avossa, and Corbetta (2007) described a progressive increase in the deactivation of the right TPJ during the search of a visual target embedded in a rapid sequence of visual distracters presented at central fixation. These authors showed that the more target occurrence was delayed, thus becoming increasingly probable along the timeline, the more TPJ was deactivated. The authors proposed that increasing TPJ deactivation reflects the filtering out of the increasing number of distracting non-target items that cumulate during the presentation of the item sequence. This first type of attentional modulation is therefore related to phasic and ongoing changes in the probability of target occurrence within a single trial. A second type of attentional modulation in the level of TPJ deactivation was highlighted as a function of the reliability with which central arrow cues indicated the position of lateral targets across the entire set of trials presented in a Posner task, i.e., as a function of cue predictiveness (Doricchi, Macci, Silvetti, & Macaluso, 2010). When cues correctly predicted target position in 80% of trials, TPJ deactivation during the cue period was higher as compared with cues that predicted target position only in 50% of trials. Poorer deactivation of the right TPJ with non-predictive cues was matched with reduced filtering out of uncued locations as indicated by a drop in the costs of reorienting of attention to invalidly cued targets and in the validity effect, i.e., the RTs advantage for validly as compared with invalidly cued targets. Taken together, these findings suggest that TPJ deactivation during voluntary orienting of attention marks the probabilistic expectancy of target occurrence in time (Shulman et al., 2007) and space (Doricchi et al., 2010).

Anatomical studies have pointed out that areas of the monkey brain that are equivalent of the human TPJ, i.e., the superior temporal gyrus and the inferior parietal lobule, are important recipients of noradrenergic innervation (NE) from the locus coeruleus (LC; Foote & Morrison, 1987; Morrison & Foote, 1986). Because of this evidence, it has been proposed that the LC-NE system modulates attention-related activity in the TPJ (Aston-Jones & Cohen, 2005; Nieuwenhuis et al., 2005). On this ground, one can reasonably argue that changes in cue predictiveness that drive changes in the level of TPJ activation during orienting of attention could also produce different levels of LC-NE activity. The availability of a behavioral or physiological marker of LC-NE activity would make possible to verify the match between cue-predictiveness and LC-NE activity in healthy human participants.

Neurophysiological (Hou, Freeman, Langley, Szabadi, & Bradshaw, 2005; Morad, Lemberg, Yofe, & Dagan, 2000) and psychopharmacological (Coull et al., 2001; Phillips, Szabadi, & Bradshaw, 2000) investigations have suggested that pupil diameter is a physiological index of LC-NE activity (Rajkowski, Kubiak, & Aston-Jones, 1993). Rajkowski et al. (1993) found that in monkeys, the baseline pupil diameter recorded at the onset of each trial in a visual discrimination task, was positively correlated to the discharge frequency of the LC. More recently, Joshi, Li, Kalwani, and Gold (2016) confirmed and expanded this evidence by showing that LC activation anticipated, at a fine temporal scale, changes in pupil dilation. Spike rate in the LC was positively correlated with pupil size diameter, both during passive fixation and in response to startling sensory events. Based on the findings by Rajkowski et al. (1993), a number of studies in healthy humans have investigated whether changes in the probabilistic relationship between sensory/motor choices and rewards are associated with changes in pupil dilation (Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Jepma & Nieuwenhuis, 2011; Murphy, Robertson, Balsters, & O'connell, 2011; Preuschoff, Hart, & Einhauser, 2011). These studies were largely inspired by neurophysiological evidence showing that when the relationship between sensory/motor choices and rewards is stable, the brain remains in an exploitative mode. This mode is characterized by reduced tonic firing of the LC/NE system and by enhanced LC/NE phasic responses to events that disconfirm the on-going probabilistic choice-reward relationship. In contrast, when the same relationship undergoes continuous changes, i.e., volatility, the brain turns in an “exploratory” mode that is aimed at discovering new rules of choice-reward association (Aston-Jones & Cohen, 2005). In this case, the baseline-tonic firing of the LC/NE system gets high with a consequent reduction in the signal to noise ratio between phasic responses to behaviorally relevant events and the baseline activity. In line with these findings, studies in healthy humans highlighted a decrement in baseline pupil dilation during the exploitation of probabilistically stable choice-reward relationships together with transient increases in pupil dilation when the on-going relationship is occasionally violated. In contrast, an increment in baseline pupil dilation is found during the exploration of new or unstable choice-reward relationships (Jepma & Nieuwenhuis, 2011; Gilzenrat et al., 2010; Silvetti, Seurinck, & Verguts, 2013a; Silvetti, Seurinck, van Bochove, Verguts, 2013b).

At variance with this relatively expanded line of research, very few studies have investigated pupil dilation during endogenous orienting of spatial attention (for exogenous orienting see Gabay, Pertzov, & Henik, 2011; Mathôt, Van der Linden, Grainger, & Vitu, 2013). Using the Attentional Network Test (ANT; Petersen & Posner, 2012), Geva, Zivan, Warsha, and Olchik (2013) showed that central spatial cues increased pupil dilation as compared with central cues that provided no spatial information. Mathot et al. (2013) found that during the 1 sec period that followed the presentation of central arrow cues, higher pupil dilation was correlated with a higher reaction time (RT) advantage for validly as compared to invalidly cued targets. Binda and Murray (2015) showed that during sustained attention to lateral target positions, pupil dilation evoked by increments in the luminance of the target background was higher when these increments occurred at the attended rather than unattended position. Finally, in line with the original proposal by Kahneman (1973), in a combined