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Research Report

Temperament and probabilistic predictive coding in visual-spatial attention





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ABSTRACT

Cholinergic (Ach), Noradrenergic (NE), and Dopaminergic (DA) pathways play an important role in the regulation of spatial attention. The same neurotransmitters are also responsible for inter-individual differences in temperamental traits. Here we explored whether biologically defined temperamental traits determine differences in the ability to orient spatial attention as a function of the probabilistic association between cues and targets. To this aim, we administered the Structure of Temperament Questionnaire (STQ-77) to a sample of 151 participants who also performed a Posner task with central endogenous predictive (80 % valid/20 % invalid) or non-predictive cues (50 % valid/50 % invalid). We found that only participants with high scores in Plasticity and Intellectual Endurance showed a selective abatement of attentional costs with non-predictive cues. In addition, stepwise regression showed that costs in the non-predictive condition were negatively predicted by scores in Plasticity and positively predicted by scores in Probabilistic Thinking. These results show that stable temperamental characteristics play an important role in defining the inter-individual differences in attentional behaviour, especially in the presence of different probabilistic organisations of the sensory environment. These findings emphasize the importance of considering temperamental and personality traits in social and professional environments where the ability to control one's attention is a crucial functional skill. © 2023 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC

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1. Introduction

To cope with capacity limits in processing incoming sensory inputs, attention mechanisms allow the brain to prioritize behaviourally relevant inputs and filter out irrelevant ones (Petersen & Posner, 2012). In the visual-spatial domain, the effects of attentional facilitation have been extensively investigated through the Posner task (Posner, 1980). In this task, a central symbolic (e.g., an arrow) or a peripheral cue (e.g., a transitory flash) directs attention to the location of an ensuing target. As a result of cueing, RTs to target stimuli are faster when the cue correctly points at the target location, i.e., Valid cue, rather than when the cue points at an incorrect target location, i.e., Invalid cue. The RTs advantage for validly with respect to invalidly cued targets is defined as Validity Effect (VE). The size of the VE is larger the more cues correctly indicate the target position in a given set of trials, i.e., cue-predictiveness (Bartolomeo et al., 2007; Bowman et al., 1993; Downing, 1988; Giessing et al., 2006; Vossel et al., 2006). Importantly, the drop in the VE that is found with nonpredictive central symbolic cues (i.e., 50 % valid and 50 % invalid cues in a set of trials) is mainly linked to the abatement of attentional costs, i.e., the RTs disadvantage for invalidly cued target as respect to targets that are preceded by spatially neutral cues. In the same non-predictive condition, attentional benefits, i.e., the RTs advantage to validly as respect to

neutrally cued targets, are maintained (Doricchi et al., 2009; Hietanen et al., 2008; Lasaponara et al., 2011, 2017).

At a neural level, when compared to the predictive condition, non-predictive endogenous cueing is characterized by a reduced de-activation of the right temporo-parietal junction (Doricchi et al., 2009), which signals a corresponding reduction in the filtering out of the uncued spatial positions. At the electrophysiological level, this effect is accompanied by a reduction in the amplitude of the Lateral Attention Directing Positivity (LDAP) component, which reflects preparatory/ facilitatory effects in visual areas contralateral to the cued side of space, and in the increases of the Anterior Directing Attention Negativity (ADAN), which marks amodal mechanisms of attentional engagement in frontal areas (Doricchi et al., 2020; Lasaponara et al., 2011, 2017). As far as concern target-related EEG activity, with nonpredictive cues, the amplitude of the inhibitory P1 recorded over the hemisphere contralateral to the no-target side was reduced in response to valid targets, whereas the same inhibitory component was increased in response to invalid ones. These findings show that the probabilistic context that defines the link between cues and targets has relevant effects on the orienting of spatial attention, influencing the interaction between cuerelated facilitatory and target-related inhibitory activity.

Over the years, investigators have gained insights into the psychopharmacological correlates of spatial orienting (see Fig. 1A). Cholinergic (Ach) pathways originating from the basal

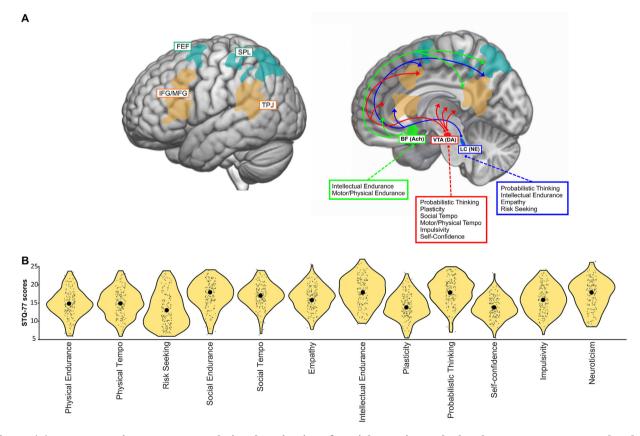


Fig. 1 - (A) Neurotransmitter systems regulating the orienting of spatial attention and related STQ-77 temperamental scales. (B) Violin plots representing the STQ-77 scores distribution for each temperamental scale; large black dots indicate median scores.

forebrain provide both phasic and tonic inputs to the attentional system (Sarter & Parikh, 2005). Phasic inputs contribute to shifts attention from monitoring for cues to cue-directed response (Howe et al., 2013). In a complementary way, tonic Ach inputs modulate phasic responses as a function of topdown demands in attentional control (Howe et al., 2013). These two mechanisms help reduce uncertainty in detecting the presence of an attention signal and favour behavioural compliance by actively representing task structure and the rules that associate attention signals with motor responses. In spatial attention, neurophysiological and psychopharmacological studies showed that the Ach activity is inversely related to the size of the VE in the Posner task (Chiba et al., 1999; Parasuraman et al., 1992; Phillips et al., 2000; Voytko et al., 1994; Whitehouse et al., 1982; Witte et al., 1997). The administration of the cholinergic agonist nicotine reduces the VE by speeding up the RTs to invalid as compared with valid targets (Murphy & Klein, 1998; Phillips et al., 2000; Stewart et al., 2001; Thiel et al., 2005; Witte et al., 1997).

The noradrenergic system (NE) originating in the locus coeruleus (LC) densely innervates the frontal, parietaltemporal cortex, and thalamus (Aston-Jones & Cohen, 2005; Foote & Morrison, 1987). The release of NE enhances the brain representation of task-relevant stimuli, i.e., "Signal", over the representation of task-irrelevant ones, i.e., "Noise". This increase in the S/N ratio determines the prioritization and attentional selection of relevant stimuli (Aston-Jones & Cohen, 2005). The LC-NE system operates under two different modalities. When stable probabilistic contingencies between events characterize the environment, the brain exploits this stability, and the LC-NE system reduces its tonic activity. In this "exploitation" mode, phasic enhancements in LC-NE activity are only elicited by events that occasionally violate established probabilistic associations within the environment. In contrast, in volatile environments characterised by poorly detectable statistical contingencies, the brain enters an "exploratory" mode that helps discover new rules and probabilistic associations between events (Aston-Jones & Cohen, 2005). During exploration, the tonic firing rate of the LC-NE system is enhanced so that the ratio between the amplitude of phasic responses to salient behavioural events and the baseline activity is reduced. The role played by the LC-NE system in orienting attention has been investigated by evaluating the effects of clonidine, an agonist of presynaptic and postsynaptic a2 receptors that inhibits the release of NE (Clark et al., 1989; Coull et al., 2001; Pliszka, 2005; Svensson et al., 1975; Witte et al., 1997), on the performance of the Posner task. In an fMRI study, Coull et al. (2001) pointed out that clonidine specifically reduces activity in the dorsal sector of the parietal cortex that is involved in the endogenous topdown guidance of visual-spatial attention rather than in reflexive re-orienting.

Another important contribution to the regulation of spatial attention is provided by the Dopaminergic (DA) innervations arising in the ventral striatum, i.e., Ventral Tegmental Area (VTA). DA is involved in the top-down regulation of attention driven by the dorsolateral prefrontal cortex and has the fundamental role of building up the brain representation of the link between sensory signals and rewards associated with these signals (Schultz, 2002, 2016; Silvetti et al., 2013). For example, brain imaging studies in humans show that the higher the release of DA in the ventral striatum, the higher the tendency to perseverate in orienting attention to sensory reward signals, even when these lose their reinforcing value (Anderson et al., 2016) or lead to adverse consequences, such as in addiction (Alcaro et al., 2021). In the monkey, injection of dopamine in the prefrontal cortex boosts the activity of ipsilateral V4 visual areas and induces a bias of attention in the contralateral direction, even when sensory stimuli are absent (Noudoost & Moore, 2011). In humans, the administration of the dopamine agonist methylphenidate increases the activity of the dorsal attentional network (e.g., IPS/SPL and FEF) during visual attention tasks (Müller et al., 2005; Tomasi et al., 2011).

Interestingly, the same pool of neurotransmitters that regulate visuo-spatial attention (see Fig. 1A) also underlie individual temperament, defined as the constitutionally-based distinctions in reactivity and self-regulation (Rothbart & Bates, 2007). In other words, according to Rothbart and Bates (2007), temperamental traits are defined by the biological bases of self-regulation processes such as effortful control and orienting of attention that, in turn, can modulate reactivity to external and internal environment. Early investigations on the relationship between neurotransmitters and constitutionally-based temperamental traits suggested a series of one-to-one correspondence between single neurotransmitters and traits (Cloninger, 1993; Depue & Collins, 1999; Gray, 1991; Netter & Rammsayer, 1991; Zuckerman, 1984). In contrast, more recent approaches consider temperament as the result of the interaction among several neurotransmitters. Trofimova and Robbins (Trofimova & Robbins, 2016) proposed a Functional Ensemble of Temperament (FET) model in which the balance of neuromodulators, such as monoamine systems, Ach, opioids, and neuropeptides, map onto the interaction between three different aspects of behaviour, i.e., maintenance, orientation and integrative functions (Trofimova & Robbins, 2016). More precisely, serotonergic (5-HT) and Ach systems are essential for maintaining the arousal needed for specific behavioural choices and inhibiting irrelevant stimuli. NE is involved in orientation to novelty and complex events, while DA is linked to integrating behavioural elements, motivation, and action initiation. Based on the level of uncertainty in the environment, these three aspects are differentially regulated by cortical or subcortical mechanisms, i.e., "cortical" contextual processing required to solve uncertainty versus "subcortical" automatic routines dealing with learned well-defined reinforcers. As a further degree of characterization, routinary behaviours could be differentially regulated whether they regard physical or social-verbal activities. Finally, this model contains three emotion-related traits attributed to dysregulation within opioid receptor systems. Individual temperamental profiles deriving from the FET model can be measured with the Structure of Temperament Questionnaire (STQ)-77 (Trofimova & Sulis, 2011), a validated self-report questionnaire that is used in the study of both clinical (Hamdioui & Vaivre-Douret, 2021; Trofimova & Sulis, 2016) and healthy participants (Trofimova, 2010).

Building on this, Posner and Rothbart (2018) suggested that the temperamental taxonomy from the FET model could represent an important clue for understanding how individual differences should be regarded in the study of attentional mechanisms (Posner & Rothbart, 2018; Rothbart & Posner, 2022). In particular, they proposed that the three major temperamental aspects of behaviour in the FET model, i.e., "maintenance", "orientation", and "integration", are respectively related to the activity of the three different attentional networks, i.e., alerting, orienting and executive control. This connection between temperament and attentional behaviour has a historical basis, with initial observations by Eysenck (1967), who suggested that introverts might have higher cortical arousal than extroverts. Successively, using the spatial orienting task, Derryberry and Reed (Derryberry & Reed, 1994) discovered that extroverts are slower in reorienting attention away from positive characteristics, while introverts are sluggish to shift away from negative ones. Along the same line, studies investigating gaze, which plays a significant role in guiding attention, discovered that personality traits are connected to eye movement and gaze direction (Isaacowitz, 2005; Rauthmann et al., 2012). More recently, using the attentional blink paradigm, some studies reported that openness and extraversion predict lower attentional blink costs than anxiety and neuroticism (Bredemeier et al., 2011; MacLean & Arnell, 2010). Altogether, these studies suggest that personality traits may be indicative of individual differences in attentional control and disengagement. However, no previous study systematically addresses the issue of inter-individual differences in attention, considering both behavioural operations and psychopharmacological aspects in the regulation of attention.

In this exploratory study, we avoided considering single temperamental traits, whose meaning in isolation is not always clear (Rothbart & Bates, 2007). Instead, we looked at the effect of the entire individual temperamental profile derived from the STQ-77 as a moderator for the attentional mechanisms. More specifically, here we explored whether biologically-defined temperamental traits determine: a) differences in the ability to orient (NE) spatial attention in contexts in which participants should learn (DA) and exploit (NE/Ach) different probabilistic association between cues and targets, b) differences in the individual adaptation (DA) to the transition from a context characterised by a stable and high probabilistic link between cues and targets, to a context characterised by a stable though probabilistically null cue-target link. It has been noted that the occurrence of an invalid target can be interpreted very differently in these two probabilistic conditions (Yu & Dayan, 2005). When cues are highly predictive, an invalid target might be interpreted as signalling that the cue-target probabilistic contingency is about to change (Yu & Dayan, 2005). In contrast, with nonpredictive cues, an invalid target is likely to be interpreted as a sort of local and expected event that brings no signal of a change in cue predictiveness (Yu & Dayan, 2005). Therefore, to better capture the online adaptation of orienting to alternating valid and invalid cues in the predictive- and non-predictive conditions, we parameterised the alternance of valid and invalid targets, and we also analysed the individual computationally defined Learning Rate (LR), which quantify the surprisal leading to belief update about cue validity.

2. Materials and methods

2.1. Participants

To determine the number of participants, before data collection, we ran a series of a-priori power analyses using G*Power software (Faul et al., 2007). In the case of repeated measures within factors ANOVA performed to check for differences in manual reaction times (RTs) from the Posner task, a minimum of 51 participants would be needed to obtain an effect size equal to f(U) = .40 considering a power of .95 and a traditional .05 alpha criterion for statistical significance. Similarly, in the case of mixed within-between ANOVAs run to check for variation in RTs as a function of the temperamental trait, a minimum of 26 participants for each group (total sample size: 52) would be needed to have a power of .95 when employing the traditional .05 alpha criterion of statistical significance. Finally, since we were interested in using STQ-77 temperamental scales as predictors for all our behavioural variables, we ran an additional power analysis for multivariate linear regression showing that at least 90 participants would be required to achieve an effect size $f^2 = .15$ considering a power of .95 and a traditional .05 alpha criterion of statistical significance.

Based on a-priori power analyses, an initial sample of two hundred and three healthy volunteers (18-to-36 years old) participated in the study. They had a normal or corrected-tonormal vision, no past or present neurological or psychiatric condition. All participants were right-handed (Edinburgh Handedness Inventory >80 %). After data acquisition, 52 participants had to be excluded from further analysis due to: I) a large number (>20 % of trial numbers) of omissions (7 participants); II) the lack of a significant Validity Effect in the Posner task (i.e., reaction times advantage for validly versus invalidly cued targets; two-tailed t-test, p < .05; 11 participants); III) an Invalid STQ-77 (see 33 participants; see paragraph 2.2.1); IV) one additional participant was excluded since his Mahalanobis distance was higher than the critical value (see paragraph 2.3.3). The final sample thus included 151 participants (35 males, 116 females; mean age: 25.2 years, SD: 5.1 years). All participants provided written informed consent to participate in the study. Experimental procedures were designed in accordance with the principles of the Declaration of Helsinki and were approved prior to data collection by the Local Ethical Committee of the Psychology Department from "Sapienza" University of Rome (Prot. n. 0002620).

2.2. Experimental procedure and tasks

All data were collected online during 2020 and 2021. A digital version of the STQ-77 was presented via Google Modules, while the presentation of stimuli and recording of manual reaction times (RTs) of the Posner task was performed with OpenSesame software (https://osdoc.cogsci.nl/3.3/). Each participant received instructions via online meetings. They were initially requested to complete the STQ-77 questionnaire and, successively, to perform the Posner task on their PC, staying about 57,5 cm from the screen and holding their gaze on central fixation throughout the experiment.

2.2.1. STQ-77

The Structure of Temperament Questionnaire (STQ-77; https://fhs.mcmaster.ca/cilab/PS/PS-STQ.htm) includes an anamnestic part and 77 question items which can be answered using a 4-point Likert scale (from 1 strongly disagree to 4 strongly agree). The anamnestic part includes questions about social status, relatives (nr. of siblings), and consumption of neuromodulators such as caffeine, alcohol, and nicotine. The question items are organized into 12 experimental scales (6 items each) and a validity scale (5 items). Experimental scales are designed to measure 12 biologically-based individual characteristics of behaviour:

- 1. **Physical Endurance** (ERM): prolonged and sustained physical effort;
- 2. Physical Tempo (TMM): speed in physical activity;
- Risk Seeking (SS): the tendency to engage in risky behaviours;
- 4. **Social Endurance** (ERS): prolonged and sustained social effort;
- Social Tempo (TMS): speed in speaking, reading or other verbal activities;
- 6. **Empathy** (EMP): sensitivity in inferring the emotional state of the other;
- 7. **Intellectual Endurance** (ERI): prolonged and sustained intellectual effort;
- Plasticity (PL): the ability to adapt quickly to plan/program changes;
- 9. **Probabilistic Thinking** (PRO): correct estimation and expectations of the probability of events;
- 10. **Self-confidence** (SLF): the tendency to optimism and confidence in one's abilities;
- 11. **Impulsivity** (IMP): lability in emotional reactions, poor immediate control of impulsive behaviours;
- 12. **Neuroticism** (NEU): poor tolerance to uncertainty with the expectation of negative situations.

The validity scale is designed to measure a social desirability tendency. The value on this scale varies from 5 to 20, and protocols with a score higher than 14 are considered invalid. For each temperamental scale, scores distribution from our sample are reported in Fig. 1B.

2.2.2. Posner task

The Posner task (see Fig. 2) was carried out in two consecutive experimental blocks of 244 trials, corresponding to the **Pre-dictive** (Pred) and **Non-Predictive** (NoPred) conditions. The Pred block was always administered before the No-Pred one.

In the Pred condition, directional cues predicted with high accuracy the spatial location of targets (80 % of Valid cues versus 20 % of Invalid cues), while in the NoPred condition, cues predicted at chance the location of targets (50 % of Valid cues versus 50 % of Invalid cues). Parameterized sequences of Valid/Invalid trials were presented pseudo-randomly. Invalid targets were presented in both experimental conditions following a series of 1-5 consecutive Valid targets (e.g., V-I, V-V-I, V-V-V-I, etc.). In the NoPred condition, to balance the number of Valid and Invalid targets, half of the sequences were composed of 1-5 Invalid targets with a Valid target presented at the end of the sequence (e.g., I-V, I-I-V, I–I–I–V, etc.). Neutral and Catch trials were always presented between each sequence in the Pred and No-Pred block. In line with previous studies that have examined learning processes that are based on inferring conditional probabilities in the time series of trials (Mengotti et al., 2017), all participants were presented with the same fixed random sequence of trials in the Pred block/condition and with another fixed sequence in the No-Pred block/condition. Before taking part in the task, all participants completed a short practice block of 32 trials. The Pred condition included 120 Valid trials, 48 Neutral trials, 40 Invalid trials and 36 Catch trials (24 directional and 12 neutral). The NoPred condition included 80 Valid trials, 48 Neutral trials, 80 Invalid trials and 36 Catch trials (24 directional and 12 neutral). In each trial, participants were asked to detect the target by pressing the keyboard spacebar with their right index finger as soon as possible and to withhold their response when no target was presented (Catch trials).

2.3. Statistical analyses

2.3.1. Analysis of manual reaction times (RTs)

Analysis of manual RTs was run to investigate, independently on the temperamental style, orienting and re-orienting of attention as a function of cue-predictiveness. Misses (RTs >2000 ms) were excluded from the analysis, mean (mi), and standard deviation (σ i) were computed for each type of trial. Trials with RTs larger than mi+2 σ i or smaller than mi-2 σ i were excluded. This procedure resulted in the exclusion of less than 2 % of manual responses. Successively, individual mean RTs were entered in a Cue Predictiveness (*Pred*, *NoPred*) × Trial type (*Valid*, *Neutral*, *Invalid*) repeated measures ANOVA. Significant main effects and interactions were explored using Bonferroni post-hoc tests.

In a second series of analyses, manual RTs from Valid and Invalid targets were analysed as a function of parameterized sequences of trials. More specifically, a Cue Predictiveness

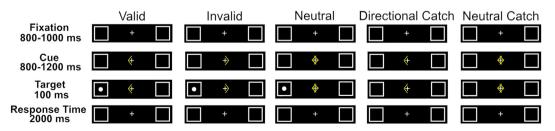


Fig. 2 – Time course of events during directional (Valid, Invalid), nondirectional (Neutral), and Catch experimental trials. The central fixation cross had a size of .5°; The two lateral boxes (1°) were cantered 4.5° to the left and the right side of the central fixation. Target was represented by a white dot (.3°).

(Pred, NoPred) × Trial type (Valid, Invalid) × Sequence (1, 2, 3, 4, 5 consecutive targets) repeated measures ANOVA was used to check whether, in the two experimental conditions, RTs in response to Valid and Invalid targets varied as a function of the number of Valid/Invalid trials that were consecutively presented. Since in the NoPred condition, half of the sequences of trials were reversed, additional Sequence type (Valid first, Invalid first) × Trial type (Valid, Invalid) × Sequence (1, 2, 3, 4, 5 consecutive targets) repeated measures ANOVA was used to compare, in the NoPred conditions, RTs to Valid and Invalid targets.

2.3.2. Analysis of learning rate (LR)

In each participant, we used the Reinforcement Meta Learner (RML) for estimating the learning rate (LR) variation during Pred and NoPred blocks (Doya et al., 2002) to quantify the surprise leading to belief update about cue validity and better capture the dynamic transition of orienting behaviour from predictive to non-predictive condition. The RML can dynamically adapt the LR based on environmental volatility and noiserelated uncertainty (Silvetti et al., 2018, 2023). The RML is a modular system that can be connected to external taskdependent modules to execute a wide variety of tasks (e.g., Silvetti et al., 2023). In this work, to simulate a Posner task, we connected the RML to a competing attractor network (Usher & McClelland, 2001). The objective of the RML was to estimate, trial by trial, the cue validity. During each trial, the RML - based on the belief in cue validity-induced a bias in the attractor network, whose role was to detect the target location. For example, if the RML estimated the current cue as invalid, it elicited a bias towards the opposite direction indicated by the cue. If the RML estimation of cue validity was correct, the RT was shorter; otherwise, it was longer. The RT was computed as a function of the network's number of cycles to converge to one attractor (see Supplementary Material). After each trial, the RML was rewarded as a linear function of the RT generated by the attractor network, so that, shorter RTs led to higher rewards, while longer RTs to smaller rewards. As we linked reward and the accuracy of cue validity estimation, the RML maximized reward by maximizing the accuracy of its beliefs about cue validity. To fit behavioural data from each human volunteer, a model inversion procedure was performed, optimizing three fixed parameters of the RML (see Supplementary Material). Optimization was done by minimizing the mean square error (MSE) between the logarithm of the inverse of the simulated RT and the actual RT using a gradient descent procedure. Afterwards, the LR was simulated trial-by-trial with the optimal parameters. Finally, successively to their estimation, LR during Pred and NoPred blocks was compared through a repeated measures ANOVA. To better catch the temporal dynamics of LR during Pred and NoPred blocks of trials, we included the first and second half of each block as a factor.

2.3.3. Relationship between STQ-77 temperamental styles and the Posner task

To investigate whether participants with opposite polarity in each temperamental trait exhibited significant differences in the behavioural performance in the Posner task, we initially divided the participants into two sub-groups with high and low scores on each STQ-77 scale. Participants were divided according to their distribution of scores around percentiles, i.e., participants were considered to have high scores whether they were placed above the 75th percentile or *low* scores in case they fell below the 25th percentile (see Supplementary Material).

RTs were then investigated through a series of twelve mixed repeated measures ANOVAs having Group (High, Low temperamental trait) as between factor, and Cue Predictiveness (Pred, NoPred) \times Trial type (Valid, Neutral, Invalid) as within factors. Significant main effects and interactions were successfully explored using Bonferroni post-hoc tests. Similarly, temperamental-induced variations in LR were analysed through a series of twelve mixed repeated measures ANOVAs having Group (High, Low temperamental trait) as between factor, and Cue Predictiveness (Pred, NoPred) \times Block phase (1 half, 2 half) as within factors.

In a second step, we further qualified the relationship between temperamental style and orienting of attention by testing whether temperamental traits could be considered predictors of behavioural indexes. We ran a series of nine stepwise linear regression analyses. The dependent variables were: Validity Effect, attentional Benefits, Costs, LR, and the Abatement of Costs (i.e., RTs difference between Costs in Pred and NoPred condition; AbC). For each regression model, independent variables consisted of the twelve STQ-77 scales and a series of covariates, i.e., Age, Sex, Cigarettes and Coffee per day, and Drink per week. Before stepwise regression analyses, all data were carefully screened for univariate and multivariate outliers. Kolmogorov-Smirnov test for data distribution and Levene's test for homoscedasticity were run to check for violation of the assumptions of normality and multicollinearity. Mahalanobis distance was calculated to detect and delete multivariate outliers. With the only exception of one participant, for all subjects, Mahalanobis distance was smaller than the critical value (all P > .001, critical value recommended by Tabachnick & Fidell, 2007). In addition, we found that variable distribution was comparable to a multivariate normal (Mardia's multivariate kurtosis index = $160.4 \le 168$; Mardia, 1970, 1974). Stepwise regressions were performed with α = .05 using SPSS (v27). Primary associations were identified as the independent predictor with the greater association with the dependent variable (i.e., the first variable listed in the regression equation). Collinearity diagnostics were monitored with variance inflation factors <5.0 considered acceptable. Z scores were used to stabilize the scales and improve the algorithm's convergence for estimating the parameters of the Gaussian mixture model.

3. Results

3.1. RTs

The ANOVA showed a significant main effect of Trial type ($F_{2,302} = 159.8$, p < .0001; $\eta_p^2 = .51$) with significant benefits (16.9 ms; p < .0001) and costs (10.6 ms; p < .0001.). A significant Cue Predictiveness \times Trial type interaction ($F_{2,302} = 70.5$, p < .0001; $\eta_p^2 = .31$) was also present. In line with a series of previous investigations from our (Doricchi et al., 2009; Dragone et al., 2018; Lasaponara et al., 2011) and other groups of research (Hietanen et al., 2008), such an interaction

revealed a selective abatement of Costs with non-predictive cueing (see Fig. 3A), while in the same experimental conditions, attentional Benefits remained unaffected. (Pred: Neutral = 325.1 vs Valid = 305.1 ms; p < .0001; NoPred: Neutral = 316.9 vs Valid = 303 ms, p < .0001). By contrast, attentional Costs were significant with predictive cues (17.9 ms) tough not with non-predictive ones (3.4 ms; Pred: Neutral = 325.1 vs Invalid = 343.1 ms, p < 0. .0001; NoPred: Neutral = 316.9 vs Invalid = 319.9 ms, p = .35).

In a second series of analyses, RTs were analysed as a function of the parameterized sequence of Valid/Invalid trials. In a first ANOVA, the presence of a significant Cue Predictiveness × Trial type × Sequence interaction ($F_{4,600} = 4.1$, p < .002; $\eta_p^2 = .05$) indicated that RTs to Invalid targets in the NoPred condition were faster, as compared to the Pred one, only when these were preceded by 2 (Pred: 255.8 vs NoPred: 240.9 ms, p = .0006) or 5 consecutive Valid targets (Pred: 251.8 vs NoPred: 242.2 ms, p = .008; see Fig. 3C). By contrast no significant differences were observed for Valid targets between the Pred and the NoPred condition. In both cases, RTs to Valid targets became progressively faster as a function of the number of targets of the same type consecutively presented (see Fig. 3C).

A second ANOVA comparing RTs in the NoPred condition as a function of sequences starting with Valid versus Invalid targets showed that compared to Invalid targets that were presented at the end of a sequence of Valid ones, responses to Invalid targets that were consecutively presented as part of a sequence were faster (Sequence type × Trial type × Sequence interaction: $F_{4,600} = 2.9$, p < .02; $\eta_p^2 = .03$; see Fig. 3C). As in the case of sequences of Valid targets, RTs to Invalid targets became progressively faster as a function of the number of targets that were consecutively presented so that, in some cases (length 1, 3 and 5), responses to Invalid were as fast as responses to Valid targets that occurred at the end of a sequence (see Fig. 3C).

3.2. LR

As shown in Fig. 4A, the RML reacted to environmental nonstationarities by increasing the LR. At the beginning of the Pred condition, the model was estimating the cue validity, and the LR was high due to the high surprisal that each trial elicited. The progressive refinement of validity estimation reduced LR as each trial became progressively less informative. The transition between Pred and NoPred conditions (vertical dotted line) led to a nonstationarity, which transitorily increased the surprisal and thence the LR. The subsequent peaks of LR during the NoPred condition were triggered by the short sequences of Invalid trials (red bars below the plot), which generated local nonstationarities in the environment. At a statistical level, a significant main effect of Cue Predictiveness ($F_{1,150} = 111.5$, p < .0001; $\eta_p^2 = .42$) showed that the LR was significantly higher in the NoPred (.18) than in the Pred (.13) experimental condition (see Fig. 4B). A significant Block Phase effect ($F_{1,150} = 713.7, p < .0001; \eta_p^2 = .82$) showed that LR dropped in the second half of the experimental block independently on the cue predictiveness, (First Half: .20 versus Second Half: .11). Nonetheless, a significant Cue Predictiveness x Block Phase interaction ($F_{1,150} = 109.5$, p < .0001; $\eta_p^2 = .42$) pointed out that the drop of LR in the second half of the experiment was stronger in the Pred than in the NoPred condition (see Fig. 4C).

3.3. RTs as a function of STQ-77 high/low scores to temperamental scales

Significant differences in RTs among the different trial types in the Pred and NoPred conditions, as a function of high or low scores in a given STQ-77 scale, are indicated by a significant Group \times Cue Predictiveness \times Trial type interaction. Such significant interactions were found for the *Plasticity* and *Intellectual Endurance* scales. More specifically, in the case of

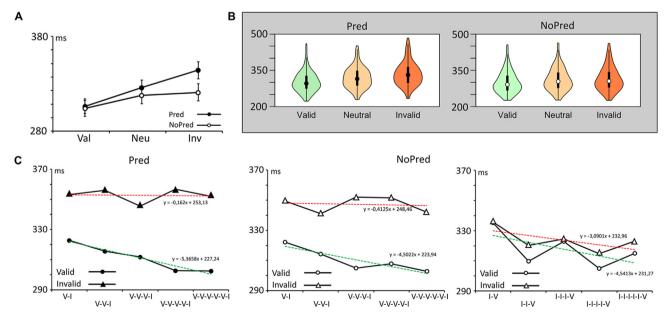


Fig. 3 – (A) Reaction Times as a function of trial type and experimental conditions. Error bars represent 95 % C.I. (B) Violin plots representing individual data's distribution, median, percentiles, and extreme points. (C) Reaction Times as a function of the parameterized sequence of Valid/Invalid trials in Pred and NoPred conditions.

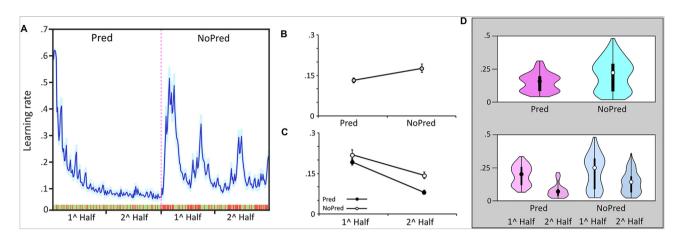


Fig. 4 – (A) LR as a function of trial number in the Pred and NoPred conditions. Green and Red bars represent Valid and Invalid trials. (B) Average LR in the Pred and NoPred conditions. Error bars represent 95 % C.I. (C) Average LR in the Pred and NoPred conditions as a function of the Block Phase (First Half versus Second Half). Error bars represent 95 % C.I. (D) Violin plots representing individual LR data's distribution, median, percentiles, and extreme points.

Plasticity, this interaction ($F_{2,148} = 8.2$, p = .0003; $\eta_p^2 = .11$) revealed that in the No-Pred condition, individuals with high Plasticity scores had a drop in attentional Costs (-12.4 ms; Neutral = 319.3 vs Invalid = 306.9 ms, p = .3) while in those with low scores Costs remained significant (19.2 ms. Neutral = 315.4 vs Invalid = 334.6 ms, p = .001; see Fig. 5A) though being reduced compared to the Pred condition (23.6 ms). No significant differences between participants with high or low Plasticity scores were found in the Pred condition.

A similar pattern of results was observed in participants with high or low scores in Intellectual Endurance ($F_{2,100} = 4.9$, p = .01; $\eta_p^2 = .1$; Fig. 5B). Also in this case, the drop in attentional Costs in the NoPred condition was only found in individuals with high scores (Costs: -1.5 ms; Neutral = 310.8 vs

Invalid = 309.3 ms, p = .6), while in those with low scores, attentional Costs remained significant in the same condition (Costs: 7.05 ms; Neutral = 317.9 vs Invalid = 325.02 ms, p = .03). Again, no significant difference between participants with high or low Intellectual Endurance was found in the Pred condition.

3.4. LR as a function of STQ-77 high/low scores to temperamental scales

A significant Group × Cue Predictiveness × Block phase interaction ($F_{1,54} = 18.2$, p < .001; $\eta_p^2 = .24$) was only found for the Risk Seeking trait. In this case, compared to participants with low scores, participants with high scores showed a

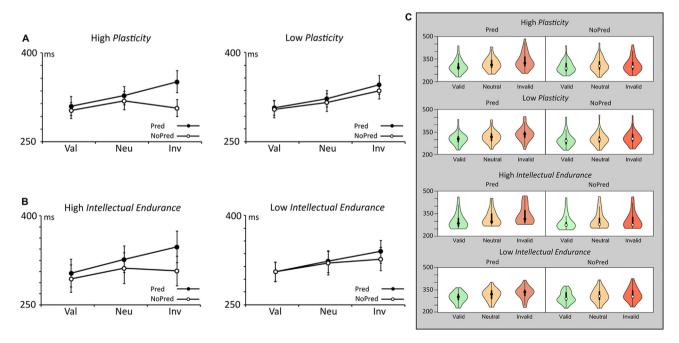


Fig. 5 – Reaction Times as a function of trial type and experimental conditions for High and Low scores to (A) Plasticiy. Error bars represent 95 % C.I. (B) Intellectual Endurance. Error bars represent 95 % C.I. (C) Violin plots representing individual data's distribution, percentiles, and extreme points.

significantly higher LR during the second half of the Pred block (High scores: 1 half = .20, 2 half = .15; Low scores 1 half = .19, 2 half = .07; see Fig. 6). No differences were observed for the NoPred block in the same participants.

3.5. Stepwise regression results

Separate stepwise regression analyses showed that Plasticity $(\beta = -.2, t_{150} = -2.5, p = .01)$ and Probabilistic Thinking ($\beta = .18$, $t_{150} = 2.3$, p = .02) were the only significant regressor to enter in a model explaining 6.7 % of the variance in the amplitude of attentional Costs in the No-Pred condition ($F_{2,150} = 5.3$, p = .006). In line with the results of the ANOVA, the zero-order correlation between Plasticity and Costs in the NoPred condition showed that the higher the scores on the scale, the smaller the attentional costs (see Fig. 7A). Conversely, the correlation between Probabilistic Thinking and non-predictive Costs indicated that higher scores in this scale were associated with higher Costs (see Fig. 7B). When Abatement of Costs was considered as the dependent variable, Self Confidence ($\beta = .16$, $t_{150} = 2.1, p = .04$) was the only significant regressor entering in a model explaining 3 % of the total variance ($F_{2,150} = 4.3$, p = .04). In this case, the zero-order correlation showed that a larger abatement of Costs in the NoPred condition was related to higher levels of Self-Confidence (see Fig. 7C).

4. Discussion

In this exploratory study, we investigated the inter-individual differences which characterize the orienting and re-orienting of spatial attention during a Posner task with central

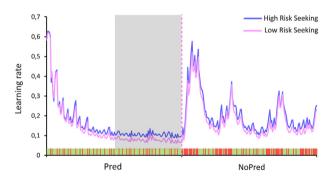


Fig. 6 – Learning Rate as a function of experimental conditions for High and Low scores to Risk Seeking scale.

endogenous cues with different levels of cue predictiveness. Specifically, we focused on individual's biologically defined temperamental traits, as described in the FET model by Trofimova and Robbins (Trofimova & Robbins, 2016), measured through the STQ-77 questionnaire (Trofimova & Sulis, 2011).

As concerns the results of the manual RTs, in line with previous observations on less numerous samples of participants (Doricchi et al., 2009, 2020; Dragone et al., 2018; Hietanen et al., 2008; Lasaponara et al., 2011), our study highlighted a selective abatement of attentional costs with non-predictive cueing. Luck et al. (Luck & Hillyard, 1994) originally described that benefits and costs are functionally separated operations. Ensuing ERPs investigations (Doricchi et al., 2020; Lasaponara et al., 2011) revealed the adaptive significance of the anatomical-functional segregation of benefits and costs, by showing that, in environments characterized by poor or null probabilistic association between cues and targets, benefits are maintained notwithstanding the speeding-up of reorienting, which is signalled by the selective abatement of Costs.

In the present study, Valid and Invalid trials were presented pseudo-randomly in a series of parametrized sequences in which an Invalid target could appear successively to a series of 1–5 Valid targets and vice versa. We found two important results when RTs were analysed as a function of these parametrized sequences.

First, independently from the experimental conditions, RTs to Valid targets become progressively faster as a function of the number of targets of the same type that were consecutively presented. Similar findings were found in a previous investigation by Huettel and co-workers (Huettel et al., 2002). In their study, the authors presented a random binary sequence of visual stimuli, each requiring a different manual response. Within this stream of presented stimuli, "repeating" (e.g., AAAAAB) and "alternating" (e.g., BABABB) patterns could implicitly and randomly occur. They found that response time in a "repeating" sequence decreased with increasing pattern length in the case of stimuli continuing a preceding pattern. At variance with this finding, response speed increased as a function of pattern length in the case of stimuli that violated the repetition of both "repeating" or "alternating" patterns. This was not the case in our study. Indeed, we found that RTs to Invalid targets presented at the end of a sequence of Valid ones were comparable among Pred and NoPred conditions and were independent of sequence length. Such a discrepancy between our results and the ones reported by Huettel et al. could be due to a difference in the maximum length of each

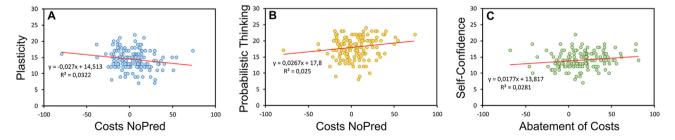


Fig. 7 – Scatterplot of correlation between attentional Costs in NoPred condition and scores in (A) Plasticity and (B) Probabilistic Thinking; (C) Correlation between the abatement of Costs in NoPred as compared to Pred condition and Self-Confidence scores.

sequence which, in their case, was composed of 1 up to 8 elements, with more pronounced statistical effects at length 5to-8. In contrast, sequences ranged from 1 to 5 elements in our work, thus possibly masking such an effect.

A second important result regards the parametrized sequences composed of a series of Invalid targets presented during the NoPred condition. As for the sequence composed of Valid targets, we found that the response speed to the Invalids becomes progressively faster as a function of sequence length. Moreover, the response speed for Valid and Invalid targets was comparable at certain lengths. These results seem to suggest that recognising local structures extracted from a series of events is an automatic, dynamic process that can overcome and contrast the costs of reorienting. Additionally, this finding provides functional characterization to the drop in attentional Costs with non-predictive cueing by pointing out that this drop could be due to the selective speeding up of manual responses when a series of Invalid targets are consecutively presented and identified as a repeating pattern within a randomly perceived trial sequence. Importantly, due to the higher number of Invalid targets presented in the NoPred condition, a series of consecutive targets of such a type could occur even when trials are presented in a fully random and not parameterized sequence, thus explaining the results observed in these previous investigations (Doricchi et al., 2009, 2020; Dragone et al., 2018; Hietanen et al., 2008; Lasaponara et al., 2011).

The findings from the analysis of the RTs in response to the different parametrized sequences of trials are nicely complemented by the study of the individual learning rate (LR). In line with predictions from the exploration/exploitation model by Yu & Dayan (2005) and from more recent neurocomputational models (Bowman et al., 2006; Samson et al., 2010; Silvetti et al., 2018), we found that LR during the initial Pred block rapidly and progressively decreased, as the observer soon learned and exploited the fixed cue-target probability of 80%V-20%I. Similarly, in the NoPred condition, participants experienced fixed cue-target probability, but in such a case, this was null (50%V-50%I). As a result, the decrease in LR was significantly lower than in the Pred condition and was characterized by "spikes" with higher LR values. These spikes were in correspondence with sequences of consecutive Invalid targets. During these sub-phases of the NoPred condition, due to the higher number of invalid events, participants might have experienced higher uncertainty thus entering in a temporary "exploratory" mode, searching for sensory evidence to confirm or disconfirm the previously established level of statistical cue-target contingencies.

4.1. Relationship between STQ-77 temperamental styles and the Posner task

Based on the analyses of individual's temperamental traits through the STQ-77, both in the case of **Plasticity** and **Intellectual Endurance**, a conventional abatement of Costs in the NoPred condition was selectively found in individuals with high scores on these scales.

According to the FET model (Trofimova & Robbins, 2016), the temperamental trait of **Plasticity** could be defined as "the ability to adapt quickly to changes in situations, to change the program of action, and to shift between different tasks". From a psychobiological point of view, recorded scores from such a scale are linked to the DA-5-HT interaction in the corticalbasal ganglia networks (Trofimova & Robbins, 2016). This proposal is supported by the results of Huettel et al. (2002), showing that violations of repeating patterns (similar to our parametrized sequences) specifically activated the basal ganglia together with the prefrontal areas. In addition, a series of recent neurocomputational investigations highlight the important role of basal ganglia in exploiting information about reward uncertainty during decision-making to maximize the expected rewards and minimize risks and losses (Gilbertson & Steele, 2021; Mikhael & Bogacz, 2016). Crucially to the aim of the present work, these studies showed that switching between exploratory and exploitative decisions is mediated by the interaction between tonic dopamine and cortical input to the basal ganglia. In these models, the tendency to seek (or avoid) options with variable reward can be controlled by increasing (or decreasing) the tonic level of dopamine. Based on these observations, individuals with lower scores on the scale of Plasticity, i.e., with a lower level of tonic DA activity in basal ganglia, might not be particularly prone to adapt their attentional behaviour to probabilistic changes occurring in the external environment and will continue to adopt an ineffective top-down strategy in the allocation of spatial attention, resulting in the maintenance of Costs.

As regard for the trait of Intellectual Endurance, this is defined as "the ability to stay focused on selected features of objects with suppression of behavioural reactivity to other features" and is linked to the activity of cortical LC-NE and ACh systems (under the lead of the NE (Trofimova & Robbins, 2016)). Previous psychopharmacological studies supported the role of LC-NE/Ach systems in focused attention (Beane & Marrocco, 2004; Dahl et al., 2022; Dalley et al., 2001; Howells et al., 2012; Klinkenberg et al., 2011; Lockhofen & Mulert, 2021; Maness et al., 2022). For example, Thiel and Fink (Thiel & Fink, 2008) observed that cholinergic agonist (nicotine) facilitates the detection of invalid targets in a conventional cueing task and reduces the associated neural activity in the inferior parietal cortex. Similarly, fMRI results from Bentley et al. (2004) showed that increasing cholinergic activity through physostigmine reduces the degree of occipital lateralization associated with directing attention to one hemifield. Thiel and Fink (2008) suggested that nicotine's effects would lead participants to rely less on cues predictiveness to orient their attention and, therefore, to a faster reorienting in case of invalid cueing. In line with this interpretation, we reported that participants with high scores in Intellectual Endurance, i.e., with higher levels of cortical LC-NE and Ach activity, showed faster re-orienting, i.e., a drop in attentional costs, when moving from Pred to NoPred condition. In contrast, such an abatement of attentional costs was lacking in participants with low scores to the same scale: as if in these participants there was a less efficient tonic firing rate of the LC-NE system during "exploration" phases in the NoPred condition. In these cases, there would be a larger difference between phasic LC-NE responses induced by salient behavioural events and a generally lower tonic/baseline activity. This, in turn, will result in a less effective cholinergic modulation that will lead

participants to slower manual RTs. This interpretation finds support in previous studies investigating spatial attention using pupil diameter (Bast et al., 2018; Dragone et al., 2018; Geva et al., 2013; Lasaponara et al., 2019; Silvetti et al., 2013), which is a reliable marker of LC-NE activity (Joshi et al., 2016; Rajkowski et al., 1994). These have reported that infrequent Invalid targets in the Pred condition elicit higher pupil dilation when compared to Valid and Neutral ones. In contrast, in the NoPred condition, with frequent Invalid targets, pupil diameter was comparable among Invalid, Neutral and Valid targets, which suggests a decrease in phasic LC-NE response to frequent Invalid stimuli (Dragone et al., 2018; Lasaponara et al., 2019). One intriguing future possibility will consist in investigating whether individual stable temperamental characteristics might also affect pupil size. In particular, it would be relevant to disambiguate whether temperamental style preferentially affects pupil variations during the cue- or the target period of a cueing task that respectively indicates modulation in the tonic and/or the phasic LC/NE activity.

When LR was analysed as a function of scores to STQ-77, we found a significant relationship between individual level in belief updating and **Risk Seeking** scores. Compared with participants characterized by risk avoidance, participants with high Risk seeking showed higher LR during the final period of the Pred block. According to the FET, Risk Seeking is defined as the "behavioural orientation to well-defined and existing sensational objects and events, underestimation of outcomes of risky behaviour" and is based on the interaction among cortisol, AdrR, DA, and PRL-NPY. Therefore, this result might suggest that it takes longer for these participants to get acquainted with statistical contingencies in the environment, so that, during the Pred block, they are prone to persist in exploring rather than exploiting the suggested cue-target associations.

Finally, stepwise regressions confirmed the negative relationship between attentional Costs in the NoPred condition and Plasticity scale by showing that the higher the scores, the less the attentional costs. The same analysis highlighted a positive relationship between Costs in the NoPred condition and Probabilistic Thinking, which is defined as "the drive to gather information about commonality, frequency and values of events, to differentiate their specific features, to project these features in future actions", and is regulated by the interaction between cortical pathways of NE, DA, 5-HT and Ach. This finding suggests that participants with a higher propensity to search for statistical rules in the environment find more disadvantageous being in an environment characterized by null probabilistic contingencies. As a result, participants with higher scores on such a scale are also characterized by higher attentional Costs during the NoPred condition. Finally, we found that in participants with higher Self-Confidence scores, the more their "sense of security – overconfidence with negligence to details", the more they could produce a drop in attentional costs when moving from the Pred to the NoPred condition. In this case, we argue that participants might benefit from their sense of security in estimating and exploiting the cue-target association rather than further exploring probabilistic contingencies in the environments.

Here we wish to consider some limitations of the present study. First, the experiment was administered online. Therefore, notwithstanding task-instructions were carefully provided via individual online meetings, we had no direct control over the maintenance of fixation or the presence of external distracting events during task performance. Nonetheless, the number of participants excluded due to a high number of omissions (n = 7; 3.4 % of the entire sample) or the absence of validity effect during the Pred condition in the Posner task (n = 11; 5.4 % of the entire sample), was relatively small. This suggests that most participants performed the task adequately. However, the exclusion of a small number of participants may have had a small impact on the reduction of inter-individual variability on the performance of the attention task in the final sample considered for the analyses.

Based on the findings from the present study, one might argue that stable temperamental traits seem to be at the base of individual differences observed in attentional behaviour. However, such a hypothesis could be biased by our experimental design in which the attention behaviour was investigated as the dependent variable at the light of individual temperamental traits that act as independent variable. An alternative plausible interpretation is that attention mechanisms serve as the foundation for individual differences in behaviour, which are then reflected in temperament (Rothbart & Bates, 2007). This suggests that temperament may be seen of as an emerging phenotype of constitutional restraints, which in turn feed off each other in a feedback loop between attention and temperament. For future investigations, it might be valuable to explore and disambiguate all these possibilities, shedding further light on the strict relationship between temperament and attentional mechanisms.

To summarise, the results from the present study demonstrate the important role of temperamental characteristics in defining the inter-individual differences in attentional behaviour. Here we have specifically focused on the interaction between interindividual differences in temperament and the adaptation of the attentional orienting system to a different probabilistic organization of the sensory environment. Future studies should address the influence of temperament on the three main components of attention, i.e., alerting, orienting and executive control (Petersen & Posner, 2012). In conclusion, our findings stress the relevance of considering individual temperamental and personality characteristics in working and social contexts where the control of attention plays an essential functional role.

CRediT authorship

SLa: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing - review and editing; GS: software, formal analysis, investigation; SLo: formal analysis, visualization; DC: resources, writing—review and editing; MC: methodology; writing—review and editing; TV: formal analysis, writing—original draft; MS: resources, supervision, writing—review and editing; FD: conceptualization, funding acquisition, methodology, project administration, supervision, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Open practice statement

The study in this article earned Open Data and Open Materials badge for transparent practices. All raw data and experimental material relative to this study are publicly available via OSF at https://osf.io/hbq96/.

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study or analyses procedures were pre-registered prior to the research being conducted. All raw data and experimental material relative to this study are publicly available via OSF at https://osf.io/hbq96/; the script for the estimation of individual learning rate using the RML model is available at: https:// github.com/AL458/RML-Posner.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2023.10.004.

REFERENCES

- Alcaro, A., Brennan, A., & Conversi, D. (2021). The seeking drive and its fixation: A neuro-psycho-evolutionary approach to the pathology of addiction. Frontiers in Human Neuroscience, 15, Article 635932. https://doi.org/10.3389/fnhum.2021.635932
- Anderson, B. A., Kuwabara, H., Wong, D. F., Gean, E. G., Rahmim, A., Brašić, J. R., George, N., Frolov, B., Courtney, S. M., & Yantis, S. (2016). The role of dopamine in value-based attentional orienting. *Current Biology*, 26(4), 550–555. https:// doi.org/10.1016/j.cub.2015.12.062
- Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. Annual Review of Neuroscience, 28, 403–450.

- Bartolomeo, P., Thiebaut de Schotten, M., & Doricchi, F. (2007). Left unilateral neglect as a disconnection syndrome. *Cerebral Cortex*, 17(11), 2479–2490. https://doi.org/10.1093/cercor/ bhl181
- Bast, N., Poustka, L., & Freitag, C. M. (2018). The locus coeruleusnorepinephrine system as pacemaker of attention—a developmental mechanism of derailed attentional function in autism spectrum disorder. European Journal of Neuroscience, 47(2), 115–125. https://doi.org/10.1111/ejn.13795
- Beane, M., & Marrocco, R. T. (2004). Norepinephrine and acetylcholine mediation of the components of reflexive attention: Implications for attention deficit disorders. Progress in Neurobiology, 74(3), 167–181. https://doi.org/10.1016/ j.pneurobio.2004.09.001
- Bentley, P., Husain, M., & Dolan, R. J. (2004). Effects of cholinergic enhancement on visual stimulation, spatial attention, and spatial working memory. *Neuron*, 41(6), 969–982. https:// doi.org/10.1016/S0896-6273(04)00145-X
- Bowman, E. M., Brown, V. J., Kertzman, C., Schwarz, U., & Robinson, D. L. (1993). Covert orienting of attention in macaques. I. Effects of behavioral context. *Journal of Neurophysiology*, 70(1), 431–443. https://doi.org/10.1152/ jn.1993.70.1.431
- Bowman, H., Schlaghecken, F., & Eimer, M. (2006). A neural network model of inhibitory processes in subliminal priming. Visual Cognition, 13(4), 401–480. https://doi.org/10.1080/ 13506280444000823
- Bredemeier, K., Berenbaum, H., Most, S. B., & Simons, D. J. (2011). Links between neuroticism, emotional distress, and disengaging attention: Evidence from a single-target RSVP task. Cognition & Emotion, 25(8), 1510–1519. https://doi.org/ 10.1080/02699931.2010.549460
- Chiba, A. A., Bushnell, P. J., Oshiro, W. M., & Gallagher, M. (1999). Selective removal of cholinergic neurons in the basal forebrain alters cued target detection. *Neuroreport*, 10(14), 3119–3123. https://doi.org/10.1097/00001756-199909290-00044
- Clark, C. R., Geffen, G. M., & Geffen, L. B. (1989). Catecholamines and the covert orientation of attention in humans. *Neuropsychologia*, 27(2), 131–139. https://doi.org/10.1016/0028-3932(89)90166-8
- Cloninger, C. R. (1993). A psychobiological model of temperament and character. Archives of General Psychiatry, 50(12), 975. https://doi.org/10.1001/archpsyc.1993.01820240059008
- Coull, J. T., Nobre, A. C., & Frith, C. D. (2001). The noradrenergic 2 agonist clonidine modulates behavioural and neuroanatomical correlates of human attentional orienting and alerting. *Cerebral Cortex*, 11(1), 73–84. https://doi.org/ 10.1093/cercor/11.1.73
- Dahl, M. J., Mather, M., & Werkle-Bergner, M. (2022). Noradrenergic modulation of rhythmic neural activity shapes selective attention. *Trends in Cognitive Sciences*, 26(1), 38–52. https://doi.org/10.1016/j.tics.2021.10.009
- Dalley, J. W., McGaughy, J., O'Connell, M. T., Cardinal, R. N., Levita, L., & Robbins, T. W. (2001). Distinct changes in cortical acetylcholine and noradrenaline efflux during contingent and noncontingent performance of a visual attentional task. The Journal of Neuroscience, 21(13), 4908–4914. https://doi.org/ 10.1523/JNEUROSCI.21-13-04908.2001
- Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. Behavioral and Brain Sciences, 22(3), 491–517. https://doi.org/10.1017/S0140525X99002046
- Derryberry, D., & Reed, M. A. (1994). Temperament and attention: Orienting toward and away from positive and negative signals. Journal of Personality and Social Psychology, 66(6), 1128–1139. https://doi.org/10.1037/0022-3514.66.6.1128
- Doricchi, F., Macci, E., Silvetti, M., & Macaluso, E. (2009). Neural correlates of the spatial and expectancy components of

endogenous and stimulus-driven orienting of attention in the Posner task. *Cerebral Cortex*, 20(7), 1574–1585.

- Doricchi, F., Pellegrino, M., Marson, F., Pinto, M., Caratelli, L., Cestari, V., Rossi-Arnaud, C., & Lasaponara, S. (2020).
 Deconstructing reorienting of attention: Cue predictiveness modulates the inhibition of the No-target side and the hemispheric distribution of the P1 response to invalid targets. Journal of Cognitive Neuroscience, 32(6), 1046–1060.
- Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *Journal of Experimental Psychology*. *Human Perception and Performance*, 14(2), 188–202.
- Doya, K., Samejima, K., Katagiri, K. I., & Kawato, M. (2002). Multiple model-based reinforcement learning. Neural Computation, 14(6), 1347–1369.
- Dragone, A., Lasaponara, S., Pinto, M., Rotondaro, F., De Luca, M., & Doricchi, F. (2018). Expectancy modulates pupil size during endogenous orienting of spatial attention. Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 102, 57–66. https://doi.org/10.1016/j.cortex.2017.09.011
- Eysenck, H. J. (1967). Personality and extra-sensory perception. Journal of the Society for Psychical Research, 44, 55–71.
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behavior Research Methods, 39(2), 175–191. https://doi.org/10.3758/BF03193146
- Foote, S. L., & Morrison, J. H. (1987). Extrathalamic modulation of cortical function. Annual Review of Neuroscience, 10(1), 67–95. https://doi.org/10.1146/annurev.ne.10.030187.000435
- Geva, R., Zivan, M., Warsha, A., & Olchik, D. (2013). Alerting, orienting or executive attention networks: Differential patters of pupil dilations. Frontiers in Behavioral Neuroscience, 7. https:// doi.org/10.3389/fnbeh.2013.00145
- Giessing, C., Thiel, C. M., Rösler, F., & Fink, G. R. (2006). The modulatory effects of nicotine on parietal cortex activity in a cued target detection task depend on cue reliability. *Neuroscience*, 137(3), 853–864. https://doi.org/10.1016/ j.neuroscience.2005.10.005
- Gilbertson, T., & Steele, D. (2021). Tonic dopamine, uncertainty and basal ganglia action selection. *Neuroscience*, 466, 109–124. https://doi.org/10.1016/j.neuroscience.2021.05.010
- Gray, J. A. (1991). The neuropsychology of temperament. In J. Strelau, A. Angleitner, & A.c. Di (Eds.), Explorations in temperament (pp. 105–128). Springer US. https://doi.org/ 10.1007/978-1-4899-0643-4_8.
- Hamdioui, S., & Vaivre-Douret, L. (2021). Investigation of clinical features of dysgraphia related to the subtypes of developmental coordination disorder in children regarding high IQ. European Psychiatry, 64(S1), S217–S218. https://doi.org/ 10.1192/j.eurpsy.2021.580
- Hietanen, J. K., Leppänen, J. M., Nummenmaa, L., & Astikainen, P. (2008). Visuospatial attention shifts by gaze and arrow cues: An ERP study. Brain Research, 1215, 123–136. https://doi.org/ 10.1016/j.brainres.2008.03.091
- Howe, W. M., Berry, A. S., Francois, J., Gilmour, G., Carp, J. M., Tricklebank, M., Lustig, C., & Sarter, M. (2013). Prefrontal cholinergic mechanisms instigating shifts from monitoring for cues to cue-guided performance: Converging electrochemical and fMRI evidence from rats and humans. The Journal of Neuroscience, 33(20), 8742–8752. https://doi.org/ 10.1523/JNEUROSCI.5809-12.2013
- Howells, F. M., Stein, D. J., & Russell, V. A. (2012). Synergistic tonic and phasic activity of the locus coeruleus norepinephrine (LC-NE) arousal system is required for optimal attentional performance. Metabolic Brain Disease, 27(3), 267–274. https:// doi.org/10.1007/s11011-012-9287-9
- Huettel, S. A., Mack, P. B., & McCarthy, G. (2002). Perceiving patterns in random series: Dynamic processing of sequence in

prefrontal cortex. Nature Neuroscience, 5(5), 485–490. https://doi.org/10.1038/nn841

- Isaacowitz, D. M. (2005). The gaze of the optimist. Personality & Social Psychology Bulletin, 31(3), 407–415. https://doi.org/ 10.1177/0146167204271599
- Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, 89(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028
- Klinkenberg, I., Sambeth, A., & Blokland, A. (2011). Acetylcholine and attention. Behavioural Brain Research, 221(2), 430–442. https://doi.org/10.1016/j.bbr.2010.11.033
- Lasaponara, S., Chica, A. B., Lecce, F., Lupianez, J., & Doricchi, F. (2011). ERP evidence for selective drop in attentional costs in uncertain environments: Challenging a purely premotor account of covert orienting of attention. *Neuropsychologia*, 49(9), 2648–2657. https://doi.org/10.1016/ j.neuropsychologia.2011.05.012
- Lasaponara, S., D' Onofrio, M., Dragone, A., Pinto, M., Caratelli, L., & Doricchi, F. (2017). Changes in predictive cuing modulate the hemispheric distribution of the P1 inhibitory response to attentional targets. *Neuropsychologia*, 99, 156–164. https://doi.org/ 10.1016/j.neuropsychologia.2017.03.010
- Lasaponara, S., Fortunato, G., Dragone, A., Pellegrino, M., Marson, F., Silvetti, M., Pinto, M., D'Onofrio, M., & Doricchi, F. (2019). Expectancy modulates pupil size both during endogenous orienting and during re-orienting of spatial attention: A study with isoluminant stimuli. European Journal of Neuroscience. https://doi.org/10.1111/ejn.14391
- Lockhofen, D. E. L., & Mulert, C. (2021). Neurochemistry of visual attention. The Florida Nurse, 15, Article 643597. https://doi.org/ 10.3389/fnins.2021.643597
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. Journal of Experimental Psychology. Human Perception and Performance, 20(5), 1000.
- MacLean, M. H., & Arnell, K. M. (2010). Personality predicts temporal attention costs in the attentional blink paradigm. Psychonomic Bulletin & Review, 17(4), 556–562. https://doi.org/ 10.3758/PBR.17.4.556
- Maness, E. B., Burk, J. A., McKenna, J. T., Schiffino, F. L., Strecker, R. E., & McCoy, J. G. (2022). Role of the locus coeruleus and basal forebrain in arousal and attention. Brain Research Bulletin, 188, 47–58. https://doi.org/10.1016/j.brainresbull.2022.07.014
- Mardia, K. V. (1970). Measures of multivariate skewness and kurtosis with applications. Biometrika, 57(3), 519–530. https:// doi.org/10.1093/biomet/57.3.519
- Mardia, K. V. (1974). Applications of some measures of multivariate skewness and kurtosis in testing normality and robustness studies.
- Mengotti, P., Dombert, P. L., Fink, G. R., & Vossel, S. (2017). Disruption of the right temporoparietal junction impairs probabilistic belief updating. The Journal of Neuroscience, 37(22), 5419–5428. https://doi.org/10.1523/JNEUROSCI.3683-16.2017
- Mikhael, J. G., & Bogacz, R. (2016). Learning reward uncertainty in the basal ganglia. Plos Computational Biology, 12(9), Article e1005062. https://doi.org/10.1371/journal.pcbi.1005062
- Müller, U., Suckling, J., Zelaya, F., Honey, G., Faessel, H., Williams, S. C. R., Routledge, C., Brown, J., Robbins, T. W., & Bullmore, E. T. (2005). Plasma level-dependent effects of methylphenidate on task-related functional magnetic resonance imaging signal changes. *Psychopharmacology*, 180(4), 624–633. https://doi.org/10.1007/ s00213-005-2264-9
- Murphy, F. C., & Klein, R. M. (1998). The effects of nicotine on spatial and non-spatial expectancies in a covert orienting task. Neuropsychologia, 36(11), 1103–1114. https://doi.org/ 10.1016/S0028-3932(98)00012-8
- Netter, P., & Rammsayer, T. (1991). Reactivity to dopaminergic drugs and aggression related personality traits. *Personality and*

Individual Differences, 12(10), 1009–1017. https://doi.org/ 10.1016/0191-8869(91)90031-6

- Noudoost, B., & Moore, T. (2011). Control of visual cortical signals by prefrontal dopamine. Nature, 474(7351), 372–375. https:// doi.org/10.1038/nature09995
- Parasuraman, R., Greenwood, P. M., Haxby, J. V., & Grady, C. L. (1992). Visuospatial attention in dementia of the Alzheimer type. Brain: a Journal of Neurology, 115(3), 711–733. https:// doi.org/10.1093/brain/115.3.711
- Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 Years after. Annual Review of Neuroscience, 35(1), 73–89. https://doi.org/10.1146/annurev-neuro-062111-150525
- Phillips, J. M., McAlonan, K., Robb, W. G. K., & Brown, V. J. (2000). Cholinergic neurotransmission influences covert orientation of visuospatial attention in the rat. Psychopharmacology, 150(1), 112–116. https://doi.org/10.1007/s002130000437
- Pliszka, S. R. (2005). The neuropsychopharmacology of attentiondeficit/hyperactivity disorder. Biological Psychiatry, 57(11), 1385–1390. https://doi.org/10.1016/j.biopsych.2004.08.026
- Posner, M. I. (1980). Orienting of attention. The Quarterly Journal of Experimental Psychology: QJEP, 32(1), 3–25. https://doi.org/ 10.1080/00335558008248231
- Posner, M. I., & Rothbart, M. K. (2018). Temperament and brain networks of attention. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1744), Article 20170254. https:// doi.org/10.1098/rstb.2017.0254
- Rajkowski, J., Kubiak, P., & Aston-Jones, G. (1994). Locus coeruleus activity in monkey: Phasic and tonic changes are associated with altered vigilance. Brain Research Bulletin, 35(5–6), 607–616. https://doi.org/10.1016/0361-9230(94)90175-9
- Rauthmann, J. F., Seubert, C. T., Sachse, P., & Furtner, M. R. (2012). Eyes as windows to the soul: Gazing behavior is related to personality. Journal of Radiological Protection: Official Journal of the Society for Radiological Protection, 46(2), 147–156. https:// doi.org/10.1016/j.jrp.2011.12.010
- Rothbart, M. K., & Bates, J. E. (2007). Temperament. In W. Damon, R. M. Lerner, & A.c. Di (Eds.), Handbook of child Psychology (p. chpsy0303). John Wiley & Sons, Inc. https://doi.org/10.1002/ 9780470147658.chpsy0303.
- Rothbart, M. K., & Posner, M. I. (2022). Individual differences in temperament and the efficiency of brain networks. Current Opinion in Behavioral Sciences, 43, 242–248. https://doi.org/ 10.1016/j.cobeha.2021.11.001
- Samson, R. D., Frank, M. J., & Fellous, J.-M. (2010). Computational models of reinforcement learning: The role of dopamine as a reward signal. Cognitive Neurodynamics, 4(2), 91–105. https:// doi.org/10.1007/s11571-010-9109-x
- Sarter, M., & Parikh, V. (2005). Choline transporters, cholinergic transmission and cognition. Nature Reviews Neuroscience, 6(1), 48–56. https://doi.org/10.1038/nrn1588
- Schultz, W. (2002). Getting formal with dopamine and reward. Neuron, 36(2), 241–263. https://doi.org/10.1016/S0896-6273(02) 00967-4
- Schultz, W. (2016). Dopamine reward prediction error coding. Dialogues in Clinical Neuroscience, 18(1), 23–32. https://doi.org/ 10.31887/DCNS.2016.18.1/wschultz
- Silvetti, M., Lasaponara, S., Daddaoua, N., Horan, M., & Gottlieb, J. (2023). A Reinforcement Meta-Learning framework of executive function and information demand. *Neural Networks*, 157, 103–113. https://doi.org/10.1016/j.neunet.2022.10.004
- Silvetti, M., Seurinck, R., & Verguts, T. (2013). Value and prediction error estimation account for volatility effects in ACC: A modelbased fMRI study. Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 49(6), 1627–1635. https://doi.org/ 10.1016/j.cortex.2012.05.008

- Silvetti, M., Seurinck, R., Bochove, M., & Verguts, T. (2013b). The influence of the noradrenergic system on optimal control of neural plasticity. Frontiers in behavioral neuroscience, 7, 160.
- Silvetti, M., Vassena, E., Abrahamse, E., & Verguts, T. (2018). Dorsal anterior cingulate-brainstem ensemble as a reinforcement meta-learner. Plos Computational Biology, 14(8), Article e1006370. https://doi.org/10.1371/ journal.pcbi.1006370
- Stewart, C., Burke, S., & Marrocco, R. (2001). Cholinergic modulation of covert attention in the rat. Psychopharmacology, 155(2), 210–218. https://doi.org/10.1007/s002130100692
- Svensson, T. H., Bunney, B. S., & Aghajanian, G. K. (1975).
 Inhibition of both noradrenergic and serotonergic neurons in brain by the α-adrenergic agonist clonidine. Brain Research, 92(2), 291–306. https://doi.org/10.1016/0006-8993(75)90276-0
- Tabachnick, B. G., & Fidell, L. S. (2007). Experimental designs using ANOVA. Thomson/Brooks/Cole.
- Thiel, C. M., & Fink, G. R. (2008). Effects of the cholinergic agonist nicotine on reorienting of visual spatial attention and topdown attentional control. *Neuroscience*, 152(2), 381–390. https://doi.org/10.1016/j.neuroscience.2007.10.061
- Thiel, C. M., Zilles, K., & Fink, G. R. (2005). Nicotine modulates reorienting of visuospatial attention and neural activity in human parietal cortex. Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology, 30(4), 810–820. https://doi.org/10.1038/sj.npp.1300633
- Tomasi, D., Volkow, N. D., Wang, G. J., Wang, R., Telang, F., Caparelli, E. C., Wong, C., Jayne, M., & Fowler, J. S. (2011). Methylphenidate enhances brain activation and deactivation responses to visual attention and working memory tasks in healthy controls. *Neuroimage*, 54(4), 3101–3110. https://doi.org/ 10.1016/j.neuroimage.2010.10.060
- Trofimova, I. (2010). An investigation into differences between the structure of temperament and the structure of personality. *The American Journal of Psychology*, 123(4), 467–480. https://doi.org/10.5406/amerjpsyc.123.4.0467
- Trofimova, I., & Robbins, T. W. (2016). Temperament and arousal systems: A new synthesis of differential psychology and functional neurochemistry. *Neuroscience and Biobehavioral Reviews*, 64, 382–402. https://doi.org/10.1016/j.neubiorev. 2016.03.008
- Trofimova, I., & Sulis, W. (2011). Is temperament activity-specific? Validation of the structure of temperament questionnairecompact. International Journal of Psychology, 11(3), 389–400.
- Trofimova, I. N., & Sulis, W. (2016). A study of the coupling of FET temperament traits with major depression. Frontiers in Psychology, 7. https://doi.org/10.3389/fpsyg.2016.01848
- Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: The leaky, competing accumulator model. Psychological *Review*, 108(3), 550–592. https://doi.org/10.1037/0033-295X.108.3.550
- Vossel, S., Thiel, C. M., & Fink, G. R. (2006). Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. *Neuroimage*, 32(3), 1257–1264. https://doi.org/10.1016/j.neuroimage.2006.05.019
- Voytko, M., Olton, D., Richardson, R., Gorman, L., Tobin, J., & Price, D. (1994). Basal forebrain lesions in monkeys disrupt attention but not learning and memory [published erratum appears in J Neurosci 1995 Mar;15(3): Following table of contents]. The Journal of Neuroscience, 14(1), 167–186. https:// doi.org/10.1523/JNEUROSCI.14-01-00167.1994
- Whitehouse, P., Price, D., Struble, R., Clark, A., Coyle, J., & DeLong, M. R. (1982). Alzheimer's disease and senile dementia: Loss of neurons in the basal forebrain. *Science*, 215(4537), 1237–1239. https://doi.org/10.1126/science.7058341

- Witte, E. A., Davidson, M. C., & Marrocco, R. T. (1997). Effects of altering brain cholinergic activity on covert orienting of attention: Comparison of monkey and human performance. *Psychopharmacology*, 132(4), 324–334. https://doi.org/10.1007/ s002130050352
- Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. Neuron, 46(4), 681–692. https://doi.org/10.1016/ j.neuron.2005.04.026
- Zuckerman, M. (1984). Sensation seeking: A comparative approach to a human trait. Behavioral and Brain Sciences, 7(3), 413–434. https://doi.org/10.1017/S0140525X00018938