

Distractors Selectively Modulate Electrophysiological Markers of Perceptual Decisions

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Abstract

■ Current models of perceptual decision-making assume that choices are made after evidence in favor of an alternative accumulates to a given threshold. This process has recently been revealed in human EEG recordings, but an unresolved issue is how these neural mechanisms are modulated by competing, yet task-irrelevant, stimuli. In this study, we tested 20 healthy participants on a motion direction discrimination task. Participants monitored two patches of random dot motion simultaneously presented on either side of fixation for periodic changes in an upward or downward motion, which could occur equiprobably in either patch. On a random 50% of trials, these periods of coherent vertical motion were accompanied by simultaneous task-irrelevant, horizontal motion in the contralateral patch. Our data

showed that these distractors selectively increased the amplitude of early target selection responses over scalp sites contralateral to the distractor stimulus, without impacting on responses ipsilateral to the distractor. Importantly, this modulation mediated a decrement in the subsequent buildup rate of a neural signature of evidence accumulation and accounted for a slowing of RTs. These data offer new insights into the functional interactions between target selection and evidence accumulation signals, and their susceptibility to task-irrelevant distractors. More broadly, these data neurally inform future models of perceptual decision-making by highlighting the influence of early processing of competing stimuli on the accumulation of perceptual evidence. ■

INTRODUCTION

Canonical models of perceptual decision-making propose that decisions are formed after perceptual evidence in favor of a given response accumulates to a given threshold (e.g., Ratcliff, Smith, Brown, & McKoon, 2016). Neurophysiological signatures of this evidence accumulation process have been observed in several areas within the rodent, monkey, and human brains (O'Connell, Shadlen, Wong-Lin, & Kelly, 2018; Shadlen & Kiani, 2013; Ding & Gold, 2011; Huk & Shadlen, 2005). Typically, however, these processes are examined in the context of perceptual decisions focused on a single stimulus. In contrast, perceptual decisions in daily life are often made in the presence of numerous stimuli that compete for processing resources and may impair the discrimination of the primary target. Although an established literature on selective attention and attentional capture has shown that distractor stimuli can interfere with target processing (Eimer, 2014; Luck, 2012; Forster & Lavie, 2011; Pashler, 1998; Posner & Petersen, 1990), an unanswered question is how the neural mechanisms underlying perceptual decision-making are modulated by competing, yet task-irrelevant, distractors.

Sequential sampling models of evidence accumulation have provided accurate accounts of perceptual decision-making behavior (Ratcliff et al., 2016; Forstmann, Wagenmakers, Eichele, Brown, & Serences, 2011), and neural signals exhibiting the predicted dynamics of evidence accumulation have recently been isolated in humans using EEG (Murphy, Boonstra, & Nieuwenhuis, 2016; Philiastides, Heekeren, & Sajda, 2014; de Lange, Rahnev, Donner, & Lau, 2013; O'Connell, Dockree, & Kelly, 2012). In particular, recent studies have established that the centroparietal positivity (CPP) builds at an evidence-dependent, RT-predictive rate that peaks immediately before response execution and exhibits amplitude modulations consistent with boundary adjustments (Kelly, Corbett, & O'Connell, 2019; Steinemann, O'Connell, & Kelly, 2018; Newman, Loughnane, Kelly, O'Connell, & Bellgrove, 2017; Kelly & O'Connell, 2013; O'Connell et al., 2012). A notable feature of the CPP is that its representation of cumulative evidence is abstracted from the specific sensory or motor requirements of the task (Twomey, Kelly, & O'Connell, 2016; O'Connell et al., 2012).

Although studies on perceptual decision-making have focused on how evidence accumulation modulates properties of the CPP, much less is known about the role of earlier target selection signals. Shortly after target onset, but before the onset of evidence accumulation, recent reports have shown an early, negative deflection over posterior electrodes. This N2 response is not merely a sensory-

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evoked response—rather, previous studies show that it is elicited only by goal-relevant sensory changes (Newman et al., 2017; Loughnane et al., 2016). The N2 exhibits distinct components over both hemispheres. When target stimuli are lateralized, there is an enhancement of the N2 contralateral to the target (the N2c), which predicts RT via a relationship with the onset and buildup rate of the CPP (Loughnane et al., 2016). In addition, lateralized targets are also accompanied by an N2 waveform in the ipsilateral hemisphere (the N2i)—the N2i has been shown to be sensitive to the salience of the target stimulus, but its relationship to behavior remains obscure (Loughnane et al., 2016).

Importantly, analogous N2 waveforms have been extensively described in the literature on attentional capture (Luck & Hillyard, 1994b). In this context, the N2 is typically probed with rapidly appearing, perceptually salient stimuli (Luck et al., 2006; Luck & Hillyard, 1994a). Such experimental designs have been useful in delineating the response properties of N2 signals in visual search, showing a positive relationship between search set size and N2 signal amplitude (Luck, 2012; Mazza, Turatto, & Caramazza, 2009). However, these studies were not optimized to isolate and measure the gradual accumulation of sensory evidence that characterizes a perceptual decision, at least in part because of the overlap between target selection signals and visual-evoked potentials triggered by abrupt stimulus onsets. Furthermore, target processing in studies on attentional capture is often focused on the difference between contralateral and ipsilateral N2 waveforms (the classic “N2pc”). Such studies usually demonstrate an enhancement of the N2pc in the presence of nontarget stimuli in visual search tasks (Eimer, 1996). However, a limitation of such an approach is that it may overlook lateralized, hemisphere-specific contributions to target and distractor processing (Schneider, Beste, & Wascher, 2012; Hickey, McDonald, & Theeuwes, 2006).

Overall, although previous studies have shown that the N2pc is modulated by distractors, the mechanism underlying this effect remains unclear. Traditional studies on attentional capture are limited in their capacity to examine the

independent contributions of the ipsilateral and contralateral N2 in the absence of overlapping visual-evoked potentials and have not examined how distractor-mediated effects on the N2 impact on subsequent evidence accumulation. Here, we examined the effects of distractor stimuli on electrophysiological markers of human perceptual decisions. Participants discriminated the direction of coherent dot motion in one hemifield, in the presence or absence of task-irrelevant distractor motion in the contralateral hemifield. We measured neural activity with EEG and asked how distractor stimuli modulated critical components of perceptual decisions, including the initial detection of the target stimulus (as measured by the N2) and/or the onset or rate of evidence accumulation (the slope of the CPP). Notably in our task, transitions from random to coherent motion occurred seamlessly, without any abrupt or net changes in the energy of low-level stimulus features. This allowed us to dissect decision-related ERPs in the presence of balanced displays of target and distractor stimuli, while eliminating large sensory-evoked potentials that may have otherwise masked or confounded these signals.

METHODS

Participants

We tested 20 participants (10 women; mean age = 22.6 ± 4.8 years, range = 19–32 years; all right-handed), with normal or corrected-to-normal vision and no history of neurological or psychiatric disease. Participants were recruited and tested at Monash University, Australia, in accordance with an experimental protocol approved by Monash University Human Research Ethics Committee.

Experimental Design

We examined perceptual decision-making in the context of a prototypical motion direction discrimination task (Loughnane et al., 2016; Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Britten, & Movshon, 1989;

Figure 1. Task design.

Participants monitored two patches of dots in the left and right hemifields for intermittent periods of coherent vertical motion in one of those patches. The task was to discriminate the direction of motion (upward or downward) of coherent vertical motion whenever it occurred. These target stimuli were accompanied in the alternate patch by either persistent random dot motion (“distractor absent”) or synchronous

periods of coherent motion in the orthogonal, horizontal plane (“distractor present”). Participants were instructed to provide fast, accurate responses to the direction of vertical target motion (red arrows) and to ignore the presence of any horizontal distractor motion (blue arrows), which was entirely task irrelevant. The location of targets (left/right), the presence of distractors (present/absent), the vertical direction of target motion (up/down), and the horizontal direction of distractor motion when present (left/right) were equiprobable.

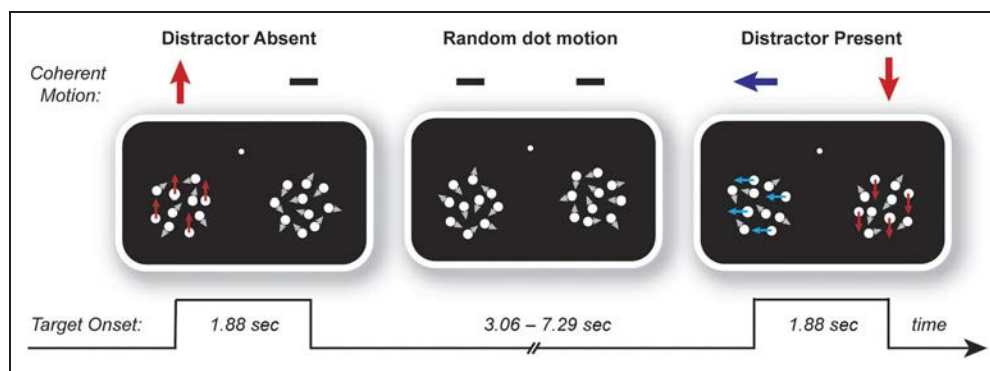


Figure 1). Participants sat in a darkened room, 70 cm from a 27-in. LCD monitor (Dell S2716DG running at 120 Hz, resolution: 1024×768). Responses were registered by button press on a Cedrus Response Pad (Model RB-840), and eye movements were monitored with an SR Research EyeLink eye tracker (DM890, EyeLink 1000 Plus Version 5.09; SR Research Ltd/SMI). The paradigm was implemented on the Psychophysics Toolbox (Brainard & Spatial Vision, 1997) run in MATLAB (MathWorks, Inc.).

Participants fixated centrally while monitoring two patches of random dot motion on either side of fixation. On all trials, dots in one patch transitioned to coherent vertical (i.e., upward or downward) motion. Participants were instructed to respond to the direction of target motion as quickly and accurately as possible with a left or right index finger button press (with response mappings counterbalanced across participants). The location (left vs. right hemifield) and direction (upward vs. downward) of target motion were equiprobable. On a random 50% of trials, the target was presented alone, in which case random dot motion persisted in the alternate patch (“distractor-absent” trials). On the remaining 50% of trials, the target motion was accompanied in the alternate patch by temporally coincident, horizontal distractor motion (leftward or rightward; “distractor present”). The direction of horizontal distractor motion was random, and participants were informed that the horizontal distractor motion was entirely uninformative and should be ignored.

Dot stimuli flickered at a rate of 30 Hz within the two patches, which were centered at 10° on either side of fixation and 4° below the horizontal meridian. Each patch subtended 8° of visual angle and comprised 150 white dots (each 6×6 pixels) against a black background. Each trial consisted of a pretarget period of random motion, lasting 3.06, 5.17, or 7.29 sec, during which dots were positioned randomly throughout each patch on each frame. During each trial, there was then a seamless step change from random motion to coherent motion, when 40% of the dots were randomly selected on each frame to be displaced by 9° s^{-1} on the following frame in the upward/downward direction (and, in the case of distractor-present trials, in the left/right direction in the alternate patch). Periods of coherent motion lasted 1.88 sec. Participants completed 16 experimental blocks of 24 trials, and trials were presented continuously without an intertrial interval. Trials that contained eye blinks or breaks of fixation of $>3^\circ$ during the entire epoch were repeated at the end of the block in random order.

EEG Acquisition and Preprocessing

Continuous EEG was acquired from 64 scalp electrodes using a Brain Products BrainVision actiCHAMP system digitized at 500 Hz. Data were processed using a combination of custom scripts and EEGLAB routines implemented in MATLAB (Delorme & Makeig, 2004). A 35-Hz fourth-order Butterworth low-pass filter was applied offline; noisy

channels were interpolated using spherical spline, and the data were rereferenced to the average reference. Epochs were extracted from the continuous data from -700 to 1880 msec around the target onset (start of the coherent motion) and were baselined with respect to -100 to 0 msec before the target onset. To limit the potential effects of volume conduction between adjacent electrodes, we transformed all signals using a current source density transformation with the CSD Toolbox for MATLAB (Kayser & Tenke, 2006).

We analyzed ERP data from the posterior N2 waveforms (N2c, N2i) and the CPP. The N2c and N2i components were measured contralateral and ipsilateral to the target patch location, respectively, from electrodes P7 and P8 (Newman et al., 2017; Loughnane et al., 2016). The CPP was measured at peak electrode CPz (Steinemann et al., 2018; Newman et al., 2017; Kelly & O’Connell, 2013). The N2pc was computed as the difference between the N2c and the N2i (N2c > N2i; Luck, 2012).

Statistical Analysis

Trials were excluded if (a) RTs were faster than 200 msec (classified as a preemptive response) or slower than 1880 msec (i.e., after coherent motion offset; classified as a missed response) or (b) recordings from any channel exceeded $\pm 100 \mu\text{V}$ from 100 msec before the target onset to 100 msec after the response. Behavioral performance was quantified by fitting RT data to an ex-Gaussian distribution using the *retimes* package in R v4.0.3 (R Foundation for Statistical Computing, Vienna, Austria). Accuracy data represent the percentage of correct trials for those trials made within the acceptable response window. These measures, as well as the ERP components, were compared between the distractor-present and distractor-absent conditions across participants using standard parametric statistics (paired *t* tests, ANOVAs). In addition to these frequentist analyses, we performed the Bayesian equivalents using the *BayesFactor* package in R v4.0.3. Bayesian analyses specified a multivariate Cauchy prior on the effects, with a distribution centered around zero and a width parameter of 0.707. Bayes factors were used to quantify evidence in favor of each hypothesis and interpreted based on Jeffreys (1961). We included subject as a random intercept in all models. Thus, the null model for all comparisons was a model including not only the grand mean but also subject as an additive factor. For the Bayesian equivalent ANOVAs, we compared the null model against the full model space of all simple effects and their interactions.

ERP analyses were performed on data from both correct and incorrect trials. All waveforms were averaged for each distractor condition. N2 peak amplitudes were defined as the most negative amplitudes after target onset within their characteristic time windows (N2c: 150–400 msec; N2i: 150–450 msec; Newman et al., 2017; Loughnane et al., 2016). In the case of the N2pc, many participants had a discernible N2pc only for the distractor-absent,

and not the distractor-present, condition. Thus, to statistically analyze the effect of distractors on the N2pc, we took the N2pc peak amplitude in the distractor-absent condition for each participant and compared it against the N2pc amplitude at that same time point for that participant in the distractor-present condition.

The CPP onsets for each participant were computed by running sample-point-by-sample-point t tests of each individual's stimulus-locked CPP amplitudes against zero. For each participant, we analyzed the distribution of CPP amplitudes across all trials, within a 100-msec window centered on each time point. The onset was defined as the first time at which the distribution of CPP amplitudes was significantly greater than zero, at a threshold of $p = .05$, for 15 or more consecutive samples from 100 to 400 msec after stimulus onset (Newman et al., 2017; Loughnane et al., 2016; O'Connell et al., 2012). The CPP slope was defined as the gradient of a straight line, fit from 450 to 50 msec before the response-locked CPP waveform, to analyze effects distal to the time interval for the N2 measurements (Loughnane et al., 2016). The CPP amplitude was measured as the mean amplitude of a 100-msec window, from -50 to $+50$ msec relative to the response.

Finally, we performed a path analysis to determine whether distractor-evoked changes in the N2 and/or CPP waveforms mediated participants' behavior (Loughnane, Newman, Tamang, Kelly, & O'Connell, 2018). The dependent variable was the RT, and the predictor variable was the absence or presence of a distractor (0 or 1). Mediating variables included the ERP components that were found to be significantly affected by the presence of a distractor in the aforementioned analyses (i.e., the N2i peak amplitude and the CPP slope). These variables were individually z scored across distractor condition. We then performed a robust path analysis with the Yuan–Bentler method and Huber–White standard errors (Ullman & Bentler, 2013). This analysis was implemented in R with the *SEM* package.

RESULTS

Behavioral Data

We examined the effect of distractors on behavioral performance by fitting RT data to an ex-Gaussian distribution. This revealed a significant effect of distractors on all RT parameters. As expected, the mean (μ) of the RT distributions was significantly greater when distractors were present versus absent (present vs. absent: mean = 827 ± 25.0 vs. 727 ± 23.2 msec), $t(19) = 8.48$, $p < .001$, $BF_{10} = 7.56 \times 10^4$ (decisive evidence). In addition, the presence of distractors led to a higher standard deviation (σ) and a lower exponential decay parameter (τ) than the distractor-absent condition (σ : present vs. absent, 171 ± 11.0 vs. 133 ± 14.0 msec; $t(19) = 5.52$, $p < .001$, $BF_{10} = 493$, decisive evidence; τ : present vs. absent, 152 ± 7.72 vs. 181 ± 7.53 msec; $t(19) = 4.44$, $p < .001$, $BF_{10} = 94$, very strong evidence). Response accuracy was numerically lower when distractors were present, but the effect did not reach statistical significance, with Bayesian analyses indicating anecdotal evidence in favor of a null effect (present vs. absent, $94.4 \pm 1.48\%$ vs. $95.3 \pm 1.46\%$), $t(19) = 1.67$, $p = .11$, $BF_{10} = 0.83$ (Figure 2).

EEG Data

Distractors Selectively Increased the Peak Negativity of the N2i but Not the N2c

First, we considered the effect of distractors on the peak amplitudes of the N2c and N2i (Figure 3). Note that the “contralateral” (N2c) and “ipsilateral” (N2i) waveforms are assigned relative to the position of the target stimulus. We performed a 2×2 repeated-measures ANOVA on the factors of Distractor (present, absent) and N2 waveform (N2c, N2i). This revealed a significant main effect of Distractor and N2, which was qualified by a significant Distractor \times N2 interaction (Distractor: $F(1, 19) = 11.9$, $p = .003$; N2: $F(1, 19) = 17.8$, $p < .001$; interaction: $F(1, 19) = 15.1$, $p = .001$). Importantly, decomposing this

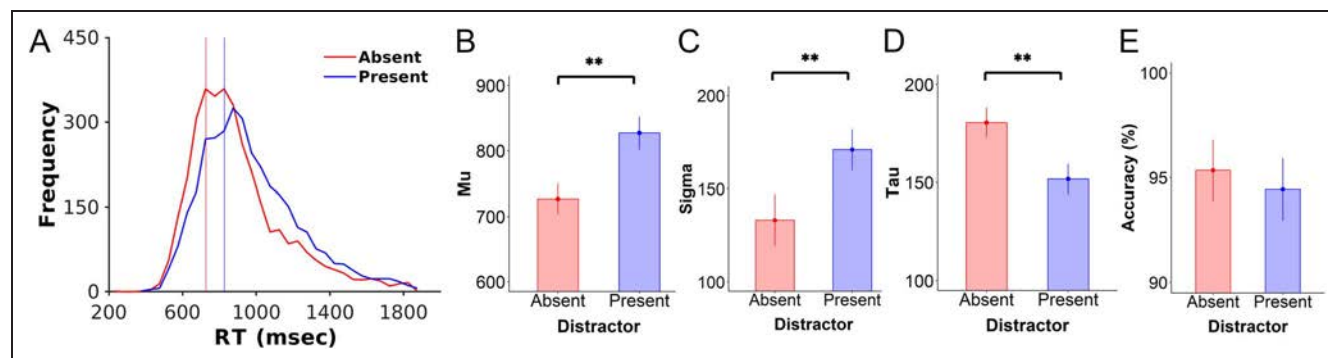


Figure 2. RTs were slower in the presence versus absence of distractors. (A) RT distributions for the distractor-absent (red) and distractor-present (blue) conditions. Vertical lines indicate mean RTs. (B–D) RT data were fit to an ex-Gaussian distribution to derive parameters for the (B) mean (μ), (C) variance (σ), and (D) exponential decay (τ) of each condition. Data showed that distractors resulted in significantly longer RTs, with greater variance and less decay than when no distractors were present. (E) Accuracy data represent the percentage of correct trials for those trials made within the acceptable response window. There were no significant differences in accuracy as a function of distractor condition. Error bars indicate 1 SEM. ** $p < .001$.

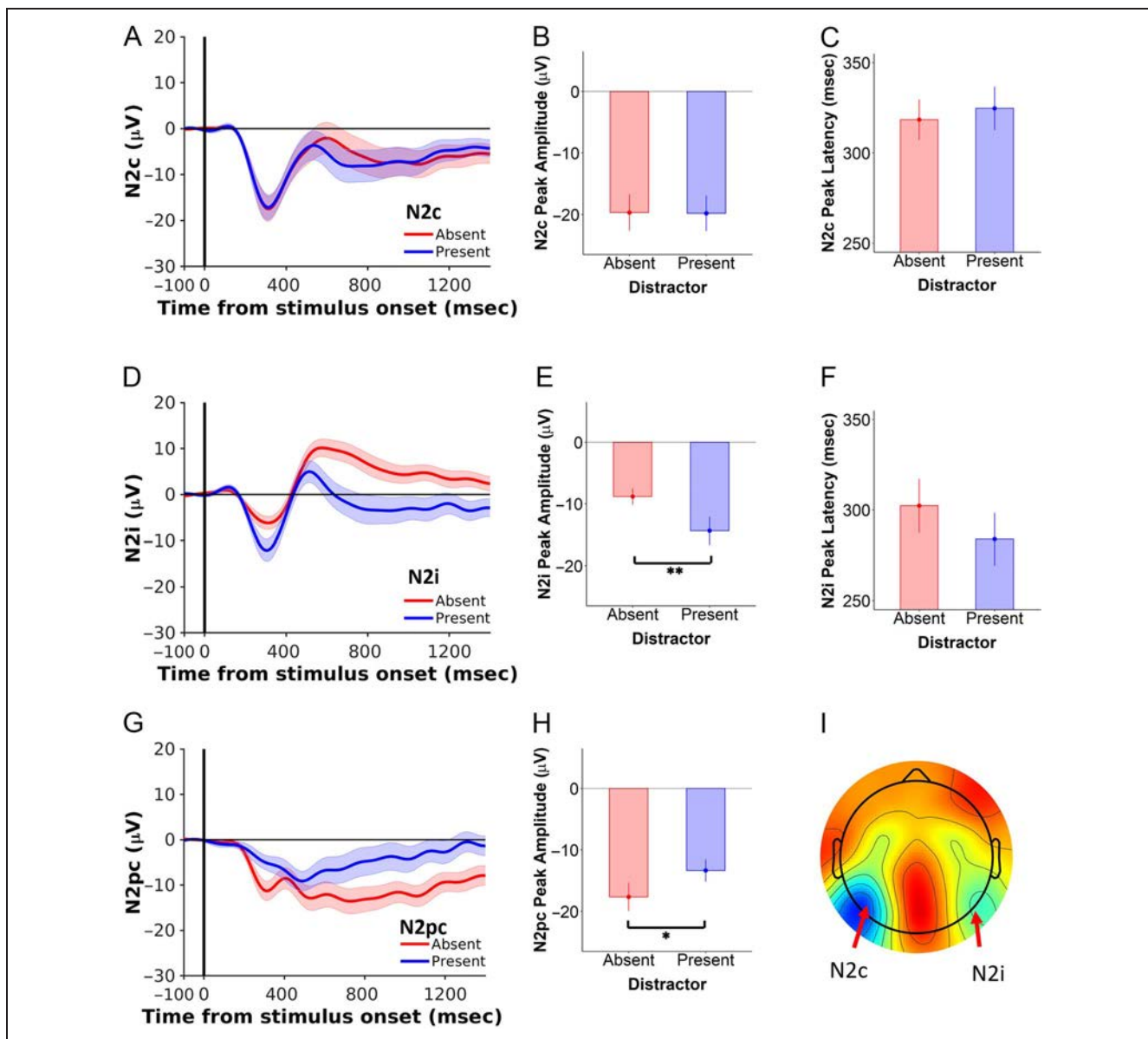


Figure 3. Distractors had a significant effect on the N2i but not the N2c. (A) The effect of distractors on the N2c waveform. ERPs are time-locked to target onset. Distractor-absent data are in red, and distractor-present data are in blue. There were no effects of distractors on mean (B) N2c peak amplitude or (C) N2c peak latency. (D) The effect of distractors on the N2i waveform. (E) Distractors led to more negative (greater amplitude) N2i peak amplitudes, (F) but there were no effects on N2i peak latency. (G, H) Distractors suppressed the N2pc peak amplitude. (I) Topographic distributions of the N2i and N2c, representing the average ERP between 200 and 400 msec after stimulus onset. The topographic plot is oriented to depict targets appearing in the right visual hemifield. Note that the N2 waveforms are defined relative to the target hemifield (i.e., the N2c is contralateral, and the N2i is ipsilateral, to the target stimulus). Thus, in our design, the N2i waveform comprises both the potential evoked by the ipsilateral target and the “N2c-like” potential evoked by the contralateral distractor. Error bars indicate 1 SEM. * $p < .05$, ** $p < .001$.

interaction with post hoc Bonferroni-corrected pairwise comparisons revealed that N2i peak amplitudes were greater (i.e., more negative) in the presence versus absence of distractors (present vs. absent, -14.06 ± 1.95 vs. -8.23 ± 1.68 μV ; $p < .001$), but there was no such effect on the N2c (present vs. absent, -19.3 ± 3.06 vs. -19.3 ± 2.71 μV ; $p = 1.0$).

The analogous Bayesian repeated-measures ANOVA revealed a similar pattern of results, showing that the data were best represented by a model that included both simple effects (Distractor and N2 waveform) and their

interaction (posterior probability of .57; $\text{BF}_{10} = 2.05 \times 10^5$). We then performed post hoc comparisons for this model (Bayesian t tests corrected for multiplicity). As in the frequentist analyses, the adjusted posteriors demonstrated very strong evidence for a difference in the N2i waveforms as a result of distractors ($\text{BF}_{10} = 96.9$), together with moderate evidence that the N2c waveforms were unaffected ($\text{BF}_{10} = 0.23$).

There was no evidence of distractor modulation of the peak latencies of the N2 waveforms. The analogous Distractor \times N2 waveform ANOVA did not reveal any

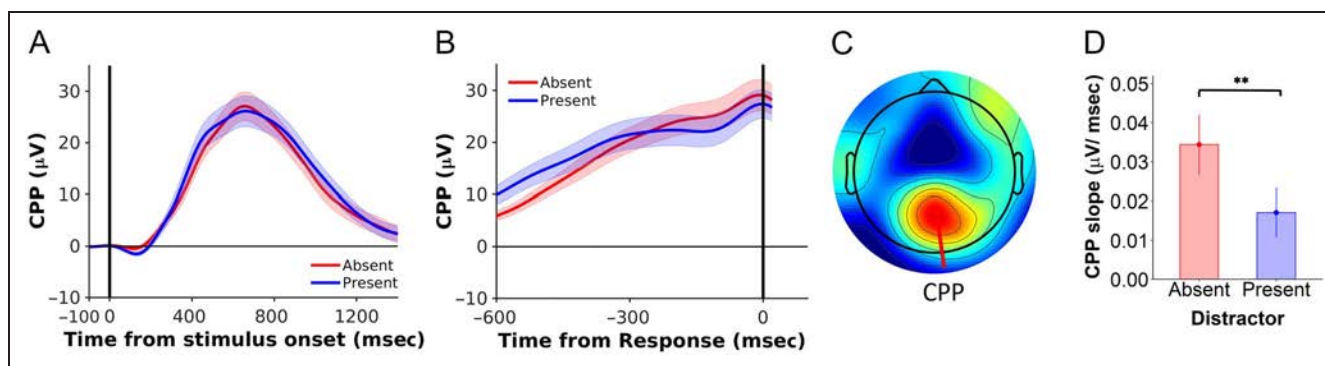


Figure 4. Distractors reduced the slope of the CPP. The CPP waveform (mean \pm 1 SEM), time-locked to (A) the stimulus onset and (B) the time of response. (C) Topographic distribution of the CPP. (D) The CPP slope was significantly lower in the presence of distractors. Distractor-absent data are in red, and distractor-present data are in blue. Error bars indicate 1 SEM. $**p < .001$.

significant effects of distractors on N2 peak latencies (Distractor: $F(1, 19) = 0.913, p = .35$; N2, $F(1, 19) = 2.39, p = .14$; Distractor \times N2: $F(1, 19) = 3.47, p = .08$). Bayesian analyses showed that the data were best fit by a model that only included the simple effect of N2 waveform, excluding the simple effect of Distractor or its interaction with N2 waveform (posterior probability of .60; $BF_{10} = 3.67$).

Prior studies on target discrimination in the context of visual search have described an N2pc waveform (Luck, 2012; Eimer, 1996), which recent studies show can be derived as a difference wave between the N2c and the N2i (Loughnane et al., 2016). To interpret our findings in the context of this work, we derived an N2pc difference wave from our recordings (N2c > N2i) and performed a paired t test on the effect of distractors on the N2pc peak amplitude (Figure 3). As expected from the lateralized N2 responses reported above, distractors led to a lower N2pc peak amplitude than when no distractors were present (present vs. absent, -12.7 ± 1.85 vs. -16.9 ± 2.35 μ V), $t(19) = 10.2, p = .024, BF_{10} = 2.41$. In the context of the preceding analyses, this difference was clearly driven by the distractor-sensitive N2i component.

Distractors Reduced the CPP Slope

Next, we considered the effects of distractors on the rate of evidence accumulation, operationalized here as the slope of the CPP (Figure 4). We measured the CPP slope in the time window 50–450 msec before response, to analyze effects distal to the time interval for the N2 measurements (Loughnane et al., 2016). Importantly, there was decisive evidence that the CPP slope was shallower in the presence versus absence of distractors (present vs. absent, $17.1 \times 10^{-3} \pm 6.30 \times 10^{-3}$ vs. $34.3 \times 10^{-3} \pm 7.77 \times 10^{-3}$ μ V msec $^{-1}$), $t(19) = 5.07, p < .001, BF_{10} = 219$. There was no significant effect of distractors on stimulus-locked CPP onsets, $t(19) = 1.95, p = .07, BF_{10} = 1.73$. There was a borderline effect of distractors on reducing CPP peak amplitudes ($t(19) = 2.23, p = .04, BF_{10} = 3.34$),

but this effect was not replicable in a follow-up experiment (see Appendix).

The Effects of Distractors on Behavior Were Significantly Mediated by N2i Peak Amplitude and CPP Slope

To summarize, the preceding analyses demonstrated that distractors significantly slowed RT and that this change in performance was accompanied first by higher amplitude N2i waveforms, followed by shallower response-locked CPP slopes. To determine whether the N2i amplitudes and CPP slopes were significant mediating variables for the effects of distractors on behavior, we performed a robust path analysis, with distractor as the predictor and RT as the outcome (Figure 5). This analysis revealed significant path coefficients between successive variables. As expected, the relationship between distractors and the N2i peak amplitude was significant in the negative direction, indicating that distractors resulted in greater negative N2i amplitudes ($a = -0.19, p < .001$). Critically, N2i peak amplitudes had a positive relationship with the CPP slope, indicating that higher amplitude (more negative) N2i amplitudes resulted in shallower CPP slopes ($b = 0.28, p = .007$). Finally, the shallower the CPP slope, the longer the RT ($c = -0.67, p < .001$). Overall, this analysis revealed that N2i peak amplitude and CPP slope partially mediated the effect of distractors on RT (total distractor–RT effect, $d = 0.29, p < .001$; direct distractor–RT effect, $d' = 0.12, p = .001$).

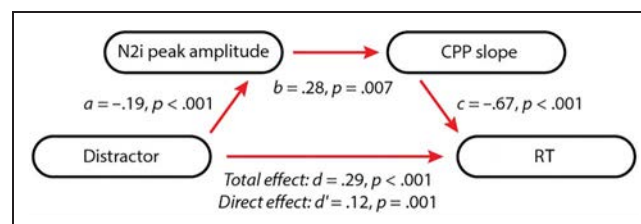


Figure 5. Path analysis showing that the effect of distractors on RT was partially mediated by the N2i peak amplitude and the CPP slope.

Results Were Replicated in a Separate Task Using Reduced Dot Densities

Finally, we examined whether these effects generalize across different viewing conditions. In a separate replication study, we asked whether our results hold when both target and distractor motion are more discriminable. Reducing the dot density of a patch of coherent motion has been shown to increase the discriminability of motion direction (Eagle & Rogers, 1997; Ramachandran & Anstis, 1983). We therefore performed a similar study to that described here, but with reduced dot densities in both target and distractor patches. This study involved a separate group of 20 healthy individuals, and the data revealed a similar pattern of results to those above. Details of this study are provided in the Appendix.

DISCUSSION

Current frameworks broadly consider perceptual decision-making to comprise several stages, from the initial representation of the sensory stimulus to the formation of a decision variable (O'Connell et al., 2018; Heekeren, Marrett, & Ungerleider, 2008). An unresolved issue is how, and at which of these stages, distractors influence a perceptual decision. We addressed this question by focusing on the rarely studied functional interactions between early target selection and evidence accumulation processes. Our key findings were that (1) distractor stimuli were accompanied by higher N2i waveforms (i.e., those ipsilateral to the target), relative to when no distractors were present; (2) these larger amplitude N2i waveforms mediated downstream effects on the CPP slope; and (3) together, these effects on the N2i and CPP mediated the effects of distractors on slowing RTs. Together, these data suggest that distractors slow perceptual decisions through selective effects on distractor processing and on the rate of evidence accumulation.

EEG markers of perceptual decision-making have typically been described in the absence of competing distractor stimuli (Kelly & O'Connell, 2013; O'Connell et al., 2012). These tasks have reported an early N2c waveform, the peak amplitude of which consistently mediates sensory evidence accumulation and behavioral performance. This has led to the proposal that the N2c is a signal reflecting early target selection (van Kempen et al., 2019; Newman et al., 2017; Loughnane et al., 2016). Our data replicate these previous findings by demonstrating a clear N2c waveform—in both the presence and absence of distractors—the peak negativity of which occurred ~300 msec after stimulus onset. In addition, however, our data add to these earlier findings by showing that the N2c waveforms are relatively insensitive to competing, concurrently presented distractor stimuli.

In contrast, distractor stimuli had robust effects on the N2i. Although the N2i has been consistently reported in perceptual decision-making tasks (van Kempen et al.,

2019; Newman et al., 2017; Loughnane et al., 2016) and is sensitive to properties of the target stimulus (e.g., its coherence), the N2i does not typically account for behavior itself (e.g., RT; Loughnane et al., 2016). An outstanding issue, therefore, has been the role of the N2i in gating the information that feeds into later stages of decision-making. The lateralized nature of our design was able to shed light on this issue. Distractors, when they appeared, were necessarily located in the hemifield contralateral to the target itself. The fact that distractors specifically enhanced the N2i, with a significantly less impact on the N2c, suggests that the N2 components generated by each hemisphere are likely to be independent.

What might this distractor-induced increase in N2i peak amplitude represent? Behaviorally, we found that distractors had a robust effect on the variance of the RT distributions, indicating a likely effect of distractors on a critical element of the decision-making process (e.g., drift rate), rather than merely a shift in nondecision time, which would have simply served to increase the mean, but not necessarily the variance, of the RT distributions. Furthermore, our key EEG result is that the distractor-mediated increases in N2i peak amplitudes led to a reduction in the rate of evidence accumulation as measured by the slope of the CPP. Importantly, this implies that higher amplitude N2i waveforms in fact related to less efficient target processing.

One explanation is that the N2i may indirectly reflect the resources consumed by an incompletely suppressed distractor stimulus—resources that are then unable to be assigned to enhance the processing of the target itself. Indeed, the nature of our distractors was such that they were events in a sensory stream that could potentially contain a target but happened not to be a target by virtue of its motion direction. Thus, it is conceivable that distractors first had to be strategically attended before being dismissed. By this account, the N2i response could represent an “N2c-like” signal evoked by the distractor stimuli and reflect the processing resources consumed by those distractors. Such an account would be consistent with perceptual load theories of attention, which propose that distractor stimuli may involuntarily capture attentional resources that are not currently allocated to target processing (Chong, Cunnington, Williams, & Mattingley, 2009; Lavie, Hirst, De Fockert, & Viding, 2004).

This interpretation might also explain our finding that distractors led to a suppression of the N2c > N2i difference wave, rather than the typical N2pc enhancement associated with distractors in visual search paradigms (Luck, 2005, 2012; Eimer, 1996). One key difference between our paradigm and visual search tasks is that the latter typically involve more perceptually salient distractor stimuli with abrupt onsets, which might require greater attentional suppression. Such suppression may result in an attenuation of the N2i waveform, leading to a net higher amplitude N2pc. This suppression may also result in a separate signal related to distractor suppression, the

distractor positivity, as has been found in other salient stimulus paradigms (Hickey, Di Lollo, & McDonald, 2009). Although we replicated the primary effects of our study with stimulus patches of reduced dot density, it may be that the discriminability of even these stimuli was lower than that of the unmasked, highly perceptually salient stimuli typically used in visual search tasks. This is suggested by the average RTs in our study (>720 msec), which were considerably longer than the mean RTs in typical visual search paradigms used to examine the N2pc (e.g., ~ 580 msec; Mazza et al., 2009). This speculation would need to be confirmed by future work, but the overall conclusion from our data emphasizes the unique importance of posterior N2 waveforms in distractor processing and in mediating the subsequent accumulation of perceptual evidence.

In summary, this study provides a first demonstration of the selective effects of task-irrelevant distractors on the neural mechanisms of evidence accumulation. Specifically, our data show how early neural processes, as measured by the N2 waveforms, are modulated by task-irrelevant distractor stimuli, and we provide evidence of the broader role of the N2i in influencing downstream perceptual evidence accumulation. Such findings invite future studies to develop more refined computational models of perceptual processing—models that may be neurally informed by electrophysiological parameters such as those described here (O’Connell et al., 2018; Purcell et al., 2010).

APPENDIX: REPLICATION EXPERIMENT WITH REDUCED PATCH DENSITIES

In a separate replication study, we asked whether the effects reported in the main text generalize across different viewing conditions. This replication study was identical to the main study, except that we increased the discriminability of target and distractor motion by reducing the dot density of target and distractor patches (Eagle & Rogers, 1997; Ramachandran & Anstis, 1983). The results of this task replicated the pattern of results from the main study.

Participants

We tested a separate group of 20 participants (12 women; mean age = 25.05 ± 5.0 years, range = 19–35 years; all right-handed), with normal or corrected-to-normal vision and no history of neurological or psychiatric disease.

Experimental Design

The task was similar to that reported in the main text. The only difference was that each patch comprised reduced dot densities of 10 dots per patch, instead of 150 in the main experiment. The analysis approach was identical to the primary analyses reported in the main text.

Results

RT data revealed the same pattern of effects as in the primary task, with distractors resulting in slower and more variable RTs relative to the distractor-absent condition (μ : present vs. absent, 817 ± 21.6 vs. 769 ± 20.2 msec, $t(19) = 4.55$, $p < .001$, $BF_{10} = 87$; σ : present vs. absent, 159 ± 6.55 vs. 135 ± 6.97 msec, $t(19) = 4.79$, $p < .001$, $BF_{10} = 150$). However, the decay parameter was similar in both distractor conditions (τ : present vs. absent, 160 ± 7.34 vs. 166 ± 8.97 msec; $t(19) = 0.92$, $p = .37$, $BF_{10} = 0.41$). Accuracy data again showed no evidence of a speed–accuracy trade-off (present vs. absent, $96.6 \pm 0.88\%$ vs. $97.3 \pm 0.57\%$; $t(19) = 1.21$, $p = .24$, $BF_{10} = 0.53$; Figure A1).

EEG Data

Distractors Selectively Increased the Peak Negativity of the N2i, but not the N2c

The corresponding Distractor (present, absent) \times N2 Waveform (N2c, N2i) repeated-measures ANOVA revealed significant main effects of Distractor and N2, which was qualified by a significant Distractor \times N2 interaction (Distractor: $F(1, 19) = 17.44$, $p < .001$; N2: $F(1, 19) = 11.12$, $p = .003$; interaction: $F(1, 19) = 7.69$, $p = .012$; Figure A2). This full

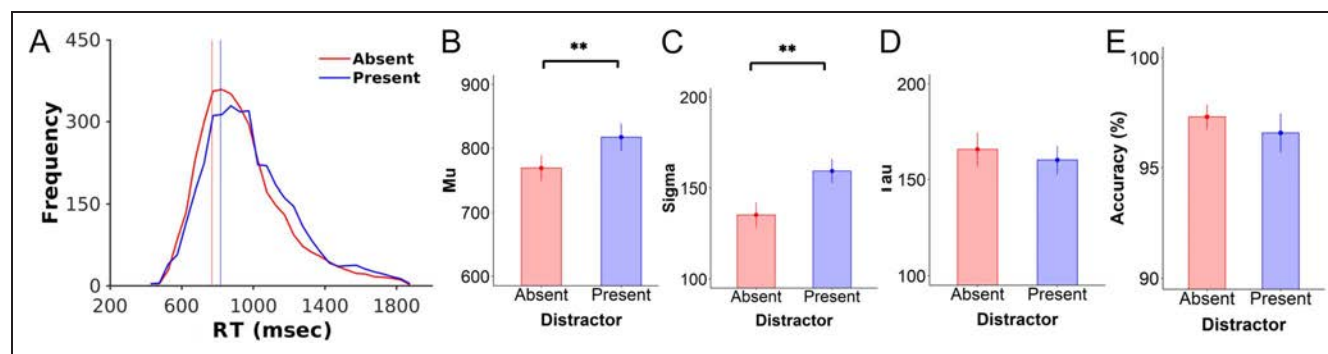


Figure A1. RTs were slower in the presence versus absence of distractors. (A) RT distributions for the distractor-absent (red) and distractor-present (blue) conditions. Vertical lines indicate mean RTs. As in the primary study, distractors led to higher (B) μ and (C) σ parameters. (D) However, the τ parameter was no different between distractor conditions. (E) There was no significant difference in accuracy between conditions. Error bars indicate 1 SEM. $**p < .001$.

model of simple effects and the interaction was also the best fitting model in the analogous Bayesian repeated-measures ANOVA (posterior probability = 0.62; $BF_{10} = 3161$). Decomposing this interaction revealed that N2i peak amplitudes were greater (i.e., more negative) in the

presence versus absence of distractors (present vs. absent, -16.57 ± 3.99 vs. $-7.69 \pm 2.22 \mu\text{V}$; $p < .001$, $BF_{10} = 36.6$). However, there was no evidence for a similar effect on the N2c (present vs. absent, -20.13 ± 3.94 vs. $-18.34 \pm 4.21 \mu\text{V}$; $p = 1.0$, $BF_{10} = 0.66$).

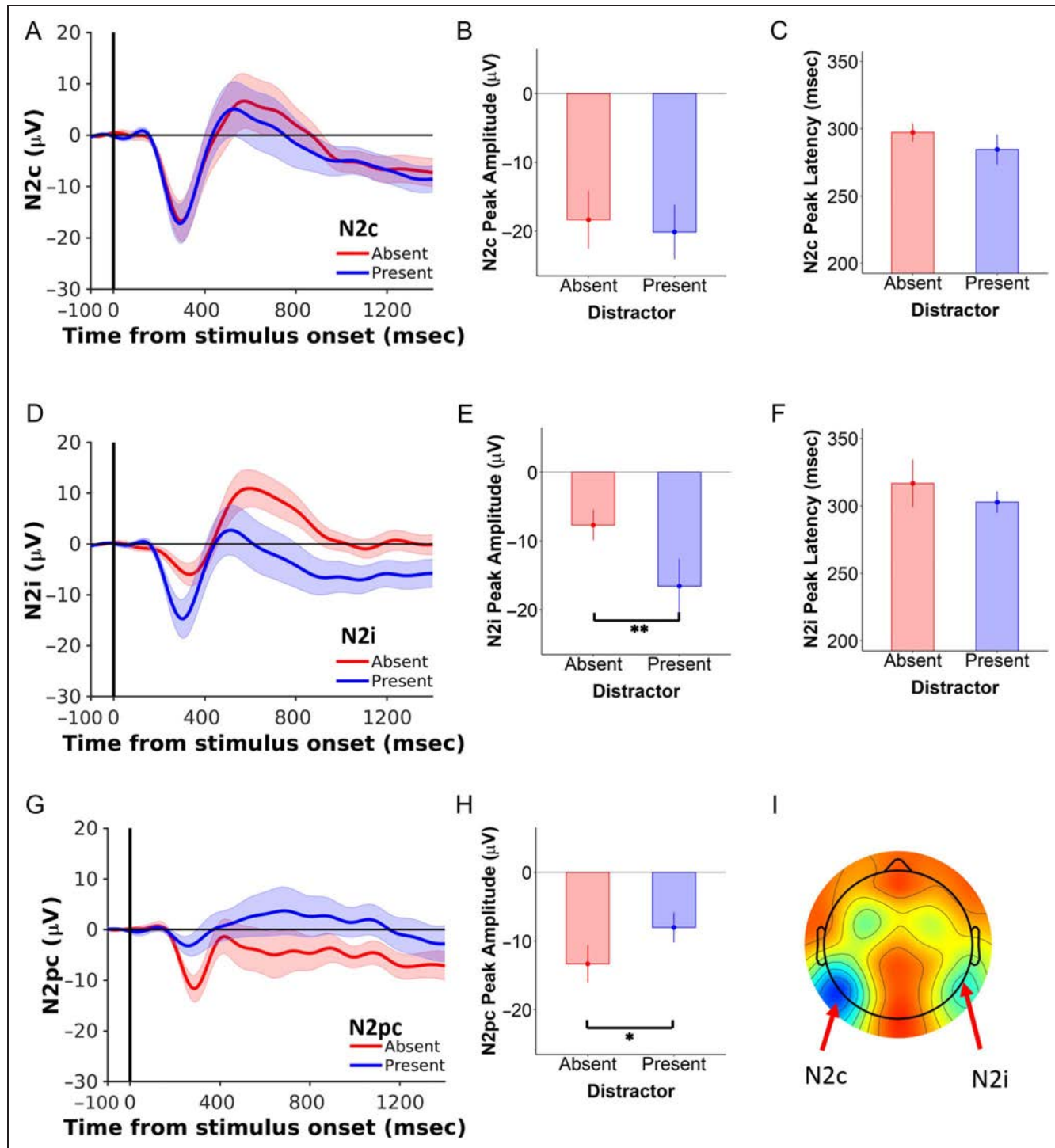


Figure A2. Distractors had a significant effect on the N2i, but not the N2c. (A) The effect of distractors on the N2c waveform. ERPs are time-locked to target onset. Distractor-absent data are in red; and distractor-present data, in blue. There were no effects of distractors on mean (B) N2c peak amplitude or (C) N2c peak latency. (D) The effect of distractors on the N2i waveform. (E) Distractors led to more negative (greater amplitude) N2i peak amplitudes, (F) but there were no effects on N2i peak latency. (G, H) Distractors suppressed the N2pc peak amplitude. (I) Topographic distributions of the N2i and N2c, representing the average ERP between 200 and 400 msec poststimulus onset. Error bars indicate 1 SEM. * $p < .05$, ** $p < .001$.

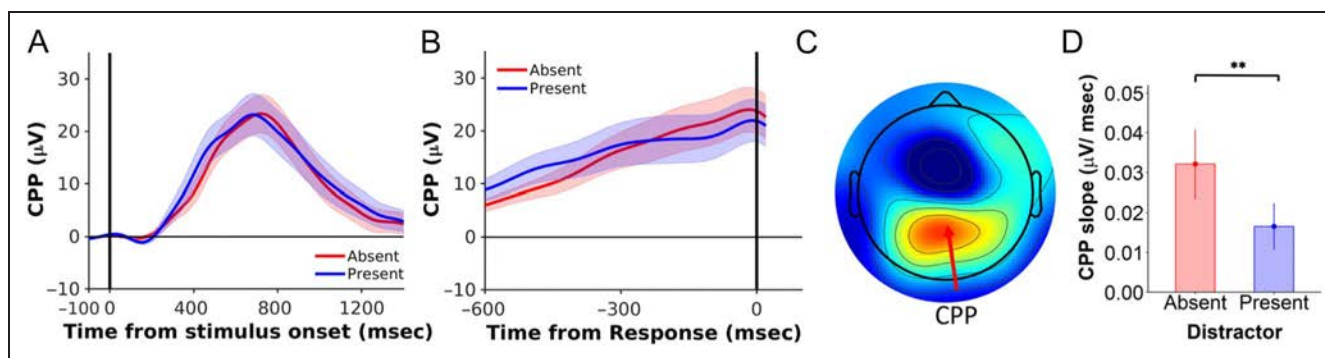
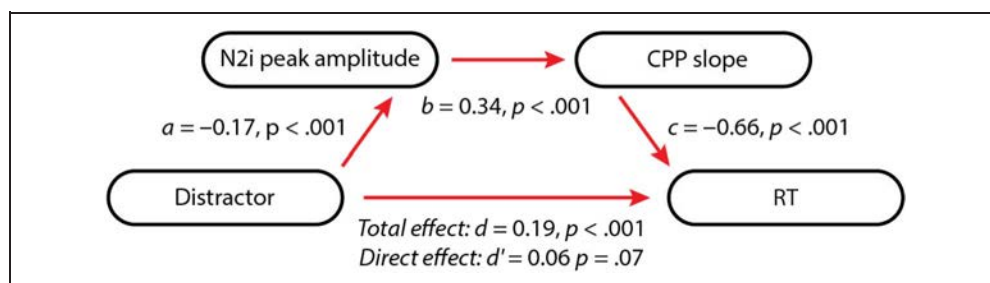


Figure A3. Distractors reduced the slope of the CPP. The CPP waveform (mean \pm 1 SEM), time-locked to (A) the stimulus onset and (B) the time of response. (C) Topographic distribution of the CPP. (D) The CPP slope was significantly lower in the presence of distractors. Distractor-absent data are in red; and distractor-present data, in blue. Error bars indicate 1 SEM. $**p < .001$.

Figure A4. Path analysis showing that the effect of distractors on RT was fully mediated by the N2i peak amplitude and CPP slope.



There was no evidence of distractor modulation of the peak latencies of the N2 waveforms. The Distractor \times N2 ANOVA did not reveal effects of distractors on N2 peak latencies (Distractor: $F(1, 19) = 1.65, p = .21$; N2: $F(1, 19) = 4.37, p = .05$; Distractor \times N2: $F(1, 19) = 0.003, p = .95$). This was reaffirmed by the Bayesian analyses, which showed that the data were best fit by a model that included only the simple effect of N2 waveform. Analyses of the N2pc again suggested a lower N2pc peak amplitude when distractors were absent versus present (present vs. absent, -8.03 ± 2.17 vs. $-13.3 \pm 2.71 \mu\text{V}$; $t(19) = 2.21, p = .04$, $\text{BF}_{10} = 1.83$).

Distractors Reduced the CPP Slope

As in the main study, distractors resulted in a significantly shallower response-locked CPP slope relative to the distractor-absent condition (present vs. absent, $16.6 \times 10^{-3} \pm 5.86 \times 10^{-3}$ vs. $32.1 \times 10^{-3} \pm 8.74 \times 10^{-3} \mu\text{V/msec}$; $t(19) = 3.40, p = .003$, $\text{BF}_{10} = 11$; strong evidence for distractor effect; Figure A3). There was again no significant evidence that distractors had an effect on CPP onsets, $t(19) = 1.45, p = .16$, $\text{BF}_{10} = 0.68$, and there was no significant evidence that distractors affected the CPP peak amplitudes, $t(19) = 1.84, p = .08$, $\text{BF}_{10} = 1.03$.

The Effects of Distractors on Behavior Were Significantly Mediated by N2i Peak Amplitude and CPP Slope

The analogous path analysis to the main study revealed a similar pattern of effects, but with a more complete

mediation effect of the N2i peak amplitude and CPP slope on RT (Figure A4). There were significant relationships between distractors and the N2i peak amplitude ($a = -0.17, p < .001$), N2i peak amplitudes and the CPP slope ($b = 0.34, p < .001$), and CPP slope and RT ($c = -0.66, p < .001$). Overall, this analysis revealed that N2i peak amplitude and CPP slope fully mediated the effect of distractors on RT (total distractor-RT effect: $d = 0.19, p < .001$; direct distractor-RT effect: $d' = 0.06, p = .07$).

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Visualization; Writing – original draft; Writing – review & editing.

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .408$, $W(\text{oman})/M = .335$, $M/W = .108$, and $W/W = .149$, the comparable proportions for the articles that these authorship teams cited were $M/M = .579$, $W/M = .243$, $M/W = .102$, and $W/W = .076$ (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

REFERENCES

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436. DOI: <https://doi.org/10.1163/156856897X00357>, PMID: 9176952

Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, 12, 4745–4765. DOI: <https://doi.org/10.1523/JNEUROSCI.12-12-04745.1992>, PMID: 1464765, PMCID: PMC6575768

Chong, T. T.-J., Cunnington, R., Williams, M. A., & Mattingley, J. B. (2009). The role of selective attention in matching observed

and executed actions. *Neuropsychologia*, 47, 786–795. DOI: <https://doi.org/10.1016/j.neuropsychologia.2008.12.008>, PMID: 19124033

de Lange, F. P., Rahnev, D. A., Donner, T. H., & Lau, H. (2013). Prestimulus oscillatory activity over motor cortex reflects perceptual expectations. *Journal of Neuroscience*, 33, 1400–1410. DOI: <https://doi.org/10.1523/JNEUROSCI.1094-12.2013>, PMID: 23345216, PMCID: PMC6618755

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9–21. DOI: <https://doi.org/10.1016/j.jneumeth.2003.10.009>, PMID: 15102499

Ding, L., & Gold, J. I. (2011). Neural correlates of perceptual decision making before, during, and after decision commitment in monkey frontal eye field. *Cerebral Cortex*, 22, 1052–1067. DOI: <https://doi.org/10.1093/cercor/bhr178>, PMID: 21765183, PMCID: PMC328342

Eagle, R. A., & Rogers, B. J. (1997). Effects of dot density, patch size and contrast on the upper spatial limit for direction discrimination in random-dot kinematograms. *Vision Research*, 37, 2091–2102. DOI: [https://doi.org/10.1016/S0042-6989\(96\)00153-8](https://doi.org/10.1016/S0042-6989(96)00153-8)

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, 99, 225–234. DOI: [https://doi.org/10.1016/0013-4694\(96\)95711-9](https://doi.org/10.1016/0013-4694(96)95711-9)

Eimer, M. (2014). The time course of spatial attention: Insights from event related brain potentials. In A. Nobre & S. Kastner (Eds.), *The Oxford handbook of attention* (1st ed., pp. 289–317). Oxford: Oxford University Press. DOI: <https://doi.org/10.1093/oxfordhb/9780199675111.013.006>

Forster, S., & Lavie, N. (2011). Entirely irrelevant distractors can capture and captivate attention. *Psychonomic Bulletin & Review*, 18, 1064–1070. DOI: <https://doi.org/10.3758/s13423-011-0172-z>, PMID: 21989770, PMCID: PMC3219870

Forstmann, B. U., Wagenmakers, E. J., Eichele, T., Brown, S., & Serences, J. T. (2011). Reciprocal relations between cognitive neuroscience and formal cognitive models: Opposites attract? *Trends in Cognitive Sciences*, 15, 272–279. DOI: <https://doi.org/10.1016/j.tics.2011.04.002>, PMID: 21612972, PMCID: PMC3384559

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, 9, 467. DOI: <https://doi.org/10.1038/nrn2374>, PMID: 18464792

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21, 760–775. DOI: <https://doi.org/10.1162/jocn.2009.21039>, PMID: 18564048

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, 18, 604–613. DOI: <https://doi.org/10.1162/jocn.2006.18.4.604>, PMID: 16768363

Huk, A. C., & Shadlen, M. N. (2005). Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *Journal of Neuroscience*, 25, 10420–10436. DOI: <https://doi.org/10.1523/JNEUROSCI.4684-04.2005>, PMID: 16280581, PMCID: PMC6725829

Jeffreys, H. (1961). *Theory of probability* (3rd ed.). Oxford: Oxford University Press.

Kayser, J., & Tenke, C. E. (2006). Principal components analysis of laplacian waveforms as a generic method for identifying erp generator patterns: I. evaluation with auditory oddball tasks. *Clinical Neurophysiology*, 117, 348–368. DOI: <https://doi.org/10.1016/j.clinph.2005.08.034>, PMID: 16356767

- Kelly, S. P., Corbett, E. A., & O'Connell, R. G. (2020). Neurocomputational mechanisms of prior-informed perceptual decision-making in humans. *Nature Human Behaviour*, *5*, 467–481. DOI: <https://doi.org/10.1038/s41562-020-00967-9>
- Kelly, S. P., & O'Connell, R. G. (2013). Internal and external influences on the rate of sensory evidence accumulation in the human brain. *Journal of Neuroscience*, *33*, 19434–19441. DOI: <https://doi.org/10.1523/JNEUROSCI.3355-13.2013>, PMID: 24336710, PMCID: PMC6618757
- Lavie, N., Hirst, A., De Fockert, J. W., & Viding, E. (2004). Load theory of selective attention and cognitive control. *Journal of Experimental Psychology: General*, *133*, 339. DOI: <https://doi.org/10.1037/0096-3445.133.3.339>, PMID: 15355143
- Loughnane, G. M., Newman, D. P., Bellgrove, M. A., Lalor, E. C., Kelly, S. P., & O'Connell, R. G. (2016). Target selection signals influence perceptual decisions by modulating the onset and rate of evidence accumulation. *Current Biology*, *26*, 496–502. DOI: <https://doi.org/10.1016/j.cub.2015.12.049>, PMID: 26853360
- Loughnane, G. M., Newman, D. P., Tamang, S., Kelly, S. P., & O'Connell, R. G. (2018). Antagonistic interactions between microsaccades and evidence accumulation processes during decision formation. *Journal of Neuroscience*, *38*, 2163–2176. DOI: <https://doi.org/10.1523/JNEUROSCI.2340-17.2018>, PMID: 29371320, PMCID: PMC6596275
- Luck, S. J. (2005). The operation of attention—Millisecond by millisecond—Over the first half second. In H. Ogmen & B. G. Breitmeyer (Eds.), *The first half second: The microgenesis and temporal dynamics of unconscious and conscious visual processes*. Cambridge, MA: MIT Press.
- Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In S. J. Luck & E. S. Kappenman (Eds.), *Oxford handbook of ERP components*. New York: Oxford University Press. DOI: <https://doi.org/10.1093/oxfordhb/9780195374148.013.0161>
- Luck, S. J., Fuller, R. L., Braun, E. L., Robinson, B., Summerfelt, A., & Gold, J. M. (2006). The speed of visual attention in schizophrenia: Electrophysiological and behavioral evidence. *Schizophrenia Research*, *85*, 174–195. DOI: <https://doi.org/10.1016/j.schres.2006.03.040>, PMID: 16713184
- Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308. DOI: <https://doi.org/10.1111/j.1469-8986.1994.tb02218.x>, PMID: 8008793
- Luck, S. J., & Hillyard, S. A. (1994b). Spatial-filtering during visual-search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014. DOI: <https://doi.org/10.1037/0096-1523.20.5.1000>
- Mazza, V., Turatto, M., & Caramazza, A. (2009). Attention selection, distractor suppression and N2pc. *Cortex*, *45*, 879–890. DOI: <https://doi.org/10.1016/j.cortex.2008.10.009>, PMID: 19084218
- Murphy, P. R., Boonstra, E., & Nieuwenhuis, S. (2016). Global gain modulation generates time-dependent urgency during perceptual choice in humans. *Nature Communications*, *7*, 13526. DOI: <https://doi.org/10.1038/ncomms13526>, PMID: 27882927, PMCID: PMC5123079
- Newman, D. P., Loughnane, G. M., Kelly, S. P., O'Connell, R. G., & Bellgrove, M. A. (2017). Visuospatial asymmetries arise from differences in the onset time of perceptual evidence accumulation. *Journal of Neuroscience*, *37*, 3378–3385. DOI: <https://doi.org/10.1523/JNEUROSCI.3512-16.2017>, PMID: 28242798, PMCID: PMC6596774
- Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*, 52–54. DOI: <https://doi.org/10.1038/341052a0>, PMID: 2770878
- O'Connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature Neuroscience*, *15*, 1729. DOI: <https://doi.org/10.1038/nn.3248>, PMID: 23103963
- O'Connell, R. G., Shadlen, M. N., Wong-Lin, K., & Kelly, S. P. (2018). Bridging neural and computational viewpoints on perceptual decision-making. *Trends in Neurosciences*, *41*, 838–852. DOI: <https://doi.org/10.1016/j.tins.2018.06.005>, PMID: 30007746, PMCID: PMC6215147
- Pashler, H. (1998). *Attention*. London: Psychology Press.
- Philiastides, M. G., Heekeren, H. R., & Sajda, P. (2014). Human scalp potentials reflect a mixture of decision-related signals during perceptual choices. *Journal of Neuroscience*, *34*, 16877–16889. DOI: <https://doi.org/10.1523/JNEUROSCI.3012-14.2014>, PMID: 25505339, PMCID: PMC4261107
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. DOI: <https://doi.org/10.1146/annurev.ne.13.030190.000325>, PMID: 2183676
- Purcell, B. A., Heitz, R. P., Cohen, J. Y., Schall, J. D., Logan, G. D., & Palmeri, T. J. (2010). Neurally constrained modeling of perceptual decision making. *Psychological Review*, *117*, 1113–1143. DOI: <https://doi.org/10.1037/a0020311>, PMID: 20822291, PMCID: PMC2979343
- Ramachandran, V. S., & Anstis, S. M. (1983). Displacement thresholds for coherent apparent motion in random-dot patterns. *Vision Research*, *23*, 1719–1724. DOI: [https://doi.org/10.1016/0042-6989\(83\)90188-8](https://doi.org/10.1016/0042-6989(83)90188-8)
- Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion decision model: Current issues and history. *Trends in Cognitive Sciences*, *20*, 260–281. DOI: <https://doi.org/10.1016/j.tics.2016.01.007>, PMID: 26952739, PMCID: PMC4928591
- Schneider, D., Beste, C., & Wascher, E. (2012). Attentional capture by irrelevant transients leads to perceptual errors in a competitive change detection task. *Frontiers in Psychology*, *3*, 164. DOI: <https://doi.org/10.3389/fpsyg.2012.00164>, PMID: 22654780, PMCID: PMC3360465
- Shadlen, M. N., & Kiani, R. (2013). Decision making as a window on cognition. *Neuron*, *80*, 791–806. DOI: <https://doi.org/10.1016/j.neuron.2013.10.047>, PMID: 24183028, PMCID: PMC3852636
- Steinmann, N. A., O'Connell, R. G., & Kelly, S. P. (2018). Decisions are expedited through multiple neural adjustments spanning the sensorimotor hierarchy. *Nature Communications*, *9*, 3627. DOI: <https://doi.org/10.1038/s41467-018-06117-0>, PMID: 30194305, PMCID: PMC6128824
- Twomey, D. M., Kelly, S. P., & O'Connell, R. G. (2016). Abstract and effector-selective decision signals exhibit qualitatively distinct dynamics before delayed perceptual reports. *Journal of Neuroscience*, *36*, 7346–7352. DOI: <https://doi.org/10.1523/JNEUROSCI.4162-15.2016>, PMID: 27413146, PMCID: PMC4945659
- Ullman, J. B., & Bentler, P. M. (2013). Structural equation modeling. In J. A. Schinka, W. F. Velicer, & I. B. Weiner (Eds.), *Handbook of psychology: Research methods in psychology* (2nd ed., pp. 661–690). Hoboken, NJ: John Wiley & Sons Inc.
- van Kempen, J., Loughnane, G. M., Newman, D. P., Kelly, S. P., Thiele, A., O'Connell, R. G., et al. (2019). Behavioural and neural signatures of perceptual decision-making are modulated by pupil-linked arousal. *eLife*, *8*, e42541. DOI: <https://doi.org/10.7554/eLife.42541>