1    **Evidence accumulation during perceptual decision-making is sensitive to the dynamics of**

2                                  **attentional selection**

*Running title:*  Decision making depends on attentional selection

*Authors:*        Dragan Rangelov[a] and Jason B. Mattingley[a,b]

*Affiliations:*

[a]Queensland Brain Institute, The University of Queensland, St Lucia, QLD 4072, Australia

[b]School of Psychology, The University of Queensland, St Lucia, QLD 4072, Australia

*Corresponding Author:*  Dragan Rangelov, d.rangelov@uq.edu.au, +61 401 281 181

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*Abstract*

The ability to select and combine multiple sensory inputs in support of accurate

decisions is a hallmark of adaptive behaviour. To date, most studies of perceptual decision-

making have involved tasks in which observers made judgements on task-relevant stimuli

only. In the real world, however, mechanisms of attention are often needed to prioritize

stimuli that are task-relevant and to attenuate potentially distracting sources of sensory

information. According to sequential-sampling decision-making models, selective attention

should modulate evidence accumulation by filtering out task-irrelevant inputs. To test this

notion, we developed a novel 'integrated' decision-making task, in which participants

judged the average direction of successive target motion signals while ignoring concurrent

and spatially overlapping distractor motion signals.  We recorded neural activity using

electroencephalography, and used computational modelling approaches to determine

whether evidence accumulation is influenced by attentional selection. We found that while

target stimuli strongly influenced perceptual decisions and associated neural activity,

concurrent and spatially coincident distractor stimuli also exerted a measurable bias on

integrated decisions and neural evidence accumulation.  Our findings suggest that

attentional selectivity dynamically modulates decision weights derived from evidence

accumulation processes, and that attention operates as a real-time but imperfect filter

between perception and decision making.

*Author summary*

The ability to decide on the basis of multiple goal-relevant signals while ignoring

distractors is a hallmark of adaptive, intelligent behaviour. While attention and decision-

making processes have been well characterised in isolation, relatively little is known about

how the two interact. Here we developed a novel paradigm in which participants had to

integrate task-relevant sensory inputs over periods of noise while disregarding distractor

signals. We demonstrate a profound influence of selective attention on behavioural and

electrophysiological measures of decision-making, and show that feature-based attention

operates as an imperfect, real-time filter between sensory inputs and decision-making

processes.

      *Introduction*

Cognition can be conceived of as a cascade of processes, beginning with the

encoding of sensory input and ending with appropriate behavioural choices. Sequential-

sampling decision-making models have had considerable success in describing choice

behaviour in terms of both behavioural performance and neural activity (1–3). According to

these models, decision-making relies on a central decision variable, an abstract quantity

that accumulates in time toward one of several possible choice alternatives. On these

accounts, a choice is made once the decision variable reaches threshold. In one widely

employed decision-making task – the random-dot motion discrimination task (2,4) (see Fig.

1a) – participants are shown fields of randomly moving dots and are asked to judge the

motion direction of a fraction of the dots that move coherently. Studies in both animals (4)

and humans (5–10) have shown that neural activity recorded during random-dot motion

discrimination follows a trajectory that resembles the accumulation of a decision variable,

thereby lending neurobiological support to sequential-sampling decision-making models.

To date, much has been learned about simple perceptual decision-making in humans

and other animal species (3,11,12). In the real world, however, decisions are often more

complex, requiring judgements on stimuli that are separated in time and space, and which

may or may not be task relevant. For example, deciding to cross a busy road requires us to

integrate the motion directions of vehicles coming from both the left and right sides, while

disregarding any movements made by people or objects on the sidewalk. Relatively little is

known about how the brain regulates decision-making when it receives competing – task-

relevant and irrelevant – sensory inputs. According to sequential-sampling decision-making

models, selective attention should mediate sensory input and evidence accumulation,

presumably filtering out task-irrelevant inputs and preventing them from being

accumulated into the decision variable (13–16). This framework raises at least two inter-

related questions. First, what is the relationship between the time-course of attentional

selection and evidence accumulation, and second, how effective is attention in mediating

sensory encoding and evidence accumulation? Conceptually, selection and accumulation

could take place sequentially so that only prioritised, task-relevant input is accumulated.

Alternatively, the two processes could take place in parallel, so that task-irrelevant inputs

might also impact upon evidence accumulation to some extent, particularly in the early

stages of attentional selection.

In recent years there has been increased interest in studying behaviour and neural

activity in more complex decision-making tasks (14,16–22). To increase decision complexity,

many of these studies have varied the number of response alternatives (e.g., two vs. four),

and have found significant costs associated with a larger number of potential responses

(e.g., Churchland et al., 2008; Leite and Ratcliff, 2010; Itthipuripat et al., 2018; Kohl et al.,

2018). As increasing response alternatives also normally requires an increase in the number

of target stimuli, it remains unclear which processing stages – from early target selection to

later response execution – are impacted by such increases in decision complexity.

Here we took a different approach by seeking to measure the effects of attention on

the dynamics of evidence accumulation using a novel task in which observers monitored

concurrent task-relevant and task-irrelevant visual stimuli. Across two experiments, we used

random-dot displays (Fig. 1a) comprising *two* simultaneous, intermingled fields of dots, one

in a cued (target) colour, the other in an uncued (distractor) colour. We presented two

epochs of concurrent target/distractor motion, and participants were asked to reproduce

the *average motion direction* of successive target-coloured dots, ignoring the directions of

any concurrent distractor dots. Thus, unlike the classical random-dot motion task in which

participants judge the direction of a single coherent motion target presented in isolation,

here they had to integrate sensory evidence from successive target motion stimuli to

determine their average direction, while trying to ignore the directions of concurrent

distractor dots. The averaging task enabled us to characterise the degree to which task-

relevant and task-irrelevant signals contribute to perceptual decision-making, and to

investigate the temporal integration of these discrete motion signals into a single,

integrated perceptual decision.

*Results*

In Experiment 1, a group of 36 participants judged the average motion direction of

target-coloured dots across three successive epochs within each trial (Fig. 1a). To quantify

task performance, we computed error magnitudes (Fig. 1b) by subtracting the true average

motion direction from the reproduced direction. The distributions of error magnitudes per

experimental condition were used to estimate the response precision ($K$) and guessing rates

($\alpha$), which reflect how well participants performed the task and how often they guessed,

respectively. As initial analyses showed no differences between repetitions and changes of

target colour within a trial (all ts < 1), these two trial types were averaged for further

analyses.

Figure 1. Schematic of the stimuli, task and the behavioural results in Experiment 1. a, Example stimulus

sequence from a typical trial (above) together with the timing of colour saturation modulation and coherent-

motion onsets (below). Participants had to reproduce the *average* motion direction of target-coloured dots by

adjusting the orientation of a response dial (black pointer). After indicating their response they received

feedback on accuracy within the same display (white pointer). b, Group-level histograms (bars) of the error

magnitude (reproduced motion direction minus expected). The pink lines show fitted distributions of target

responses and guesses using mixture-distribution modelling of each individual participant's data. c, Average

decision weights showing the contributions of each presented motion direction to the decision. Since there

were no significant differences (t < 1) between the two non-target motions in the "No target" condition (blue

bars), only the average of the two is shown. Grey dots denote individual participants.

The average response precision was high both in the one- and two-target colour

conditions ($K_{M/SEM}$ = 10.52/1.70 and 11.79/2.08), and did not differ significantly between

conditions (F < 1). Overall, the full-width-at-half-maximum (FWHM) of the fitted distribution

of target responses was around 40°. For reference, the average tuning width of individual

neurons in macaque area MT is about 60° FWHM (31). The average guessing rates ($\alpha$) were

around 26%, and did not change across experimental conditions (F < 1).

To quantify how much each of the presented target and distractor signals influenced

observers' average-motion decisions, we used linear regression modelling with complex-

valued data (see Methods). The decision weights for all motion signals in all experimental

conditions were significantly different from zero (all p < .001), indicating that both task-

relevant and task-irrelevant signals contributed to the decision. As with the mixture

distribution modelling, initial analyses of decision weights revealed no significant

differences between target colour repetitions and changes (all Fs < 1.97, all ps > .170), so

the two conditions were averaged for further analyses. Overall, the weights for targets

(.44/.01, Fig. 1c) were much higher ($F_{2,64}$ = 326.80, p < .001, $\eta_p^2$ = .91) than the weights for

either concurrently presented distractors (.19/.01) or distractors presented on their own

(.13/.01). Unexpectedly, there was also a reliable order effect, with higher target weights for

the first epoch than for the second (.50/.01 vs. .38/.02, $t_{32}$ = 4.74, p < .001); analogously,

distractor weights were lower for the first epoch than for the second (.14/.01 vs. .23/.01, $t_{32}$

= 4.68, p < .001). Overall, the analyses of decision weights revealed that attention operates

as an imperfect filter between sensory input and evidence accumulation by attenuating,

rather than eliminating, the weights associated with task-irrelevant inputs.

We next characterised the temporal dynamics of evidence accumulation. To this

end, we inspected the CPP ERP component whose time-course has been shown to closely

follow evidence accumulation (3,8–10,32). We were particularly interested in the CPP in no-

target epochs: if attentional selection and evidence accumulation operate sequentially, then

attention should suppress motion signals, predicting no CPP in this epoch. By contrast, if

selection and accumulation take place concurrently, there should be a significant CPP even

in the no-target epoch.

**Figure 2. Topography and time course of the CPP component in Experiment 1. a,** Surface-Laplacian-filtered

EEG topography averaged across all conditions at times of peak colour saturation for all three epochs (1, 3, and

5 s after stimulus onset). The markers denote the electrode pair [CPz and Cz] used for the ERP analyses. **b,**

Time-course of the CPP averaged across all experimental conditions (M ± 1 within-participants SEM; Morey,

2008) for the total trial duration. **c,** CPP time-course during the gradual increase in colour saturation, shown

separately per epoch and experimental condition. Symbols above the x-axis denote time samples for which the

voltage was significantly different from 0 at $p_{FDR} < .05$. Full-line and dashed-line arrows indicate onset latencies

in the one and two target colours conditions, respectively. For the purpose of data presentation, all traces

were low-pass filtered at 10 Hz using a 4th order Butterworth IIR filter. Data analyses were conducted using

unfiltered data.

Inspection of the ERP topographies (Fig. 2a) revealed a central-medial positivity

consistent with the usual CPP component (8). Throughout the trial, the CPP (Fig. 2b) closely

followed the time-course of colour modulation, with three distinct peaks coinciding with the

three episodes of maximum colour saturation. Between epochs, as the colour saturation of

the dots returned to grey, the CPP amplitude also returned close to baseline. This pattern

suggests that evidence was accumulated only during the informative time periods, and

implies a strong effect of attention on evidence accumulation. If evidence had accumulated

throughout the trial irrespective of task-relevance, we would have expected a sustained CPP

response, which clearly was not the case.

Next, the whole-trial epochs were divided into three segments relative to the onset

of colour saturation modulation, and baseline-corrected relative to the average of all three

epochs over a window of 100 ms prior to onset.  Thus, all three epochs had the same

baseline, permitting comparisons between them. The epochs were then sorted according to

experimental conditions (first target, second target, no target; one- and two-target colours)

and averaged across trials. As with the behavioural findings, we observed no effects of

target colour repetitions vs. changes (all $F_c < 1$). Further analyses were therefore conducted

using the average of the two trial types. Overall, there was a statistically significant positive

deflection in all experimental conditions (Fig. 2c). The onset latency (522 ms) and the CPP

slope (3.31 µV/s) were similar across experimental conditions (all $F_c < 1$), suggesting that the

rate of evidence accumulation did not differ between conditions. The peak CPP amplitude,

however, *decreased* between epochs ($F_{c(2,64)} = 46.41$, $p < .001$), from the first target epoch

to the second and then to the no-target epoch (2.74, 2.43 and 1.06 µV, respectively, all $t_{c(32)}$

$\geq 1.93$, $p \leq .031$). Finally, the number of target colours had no significant effect on the peak

CPP amplitude, either as a main effect ($F_c < 1$) or in combination with epoch ($F_{c(2,64)} = 1.44$, p

= .244).

Taken together, the results of Experiment 1 revealed strong effects of selective

attention on decision-making. At the neural level, attention had a robust effect on the peak

CPP amplitude, with higher peaks for target-present epochs than for no-target epochs.

Behaviourally, target signals were associated with significantly larger decision weights than

distractors. Importantly, however, neither the CPP onset nor the slope differed between

target-present and no-target epochs, suggesting that both task-relevant and task-irrelevant

inputs triggered evidence accumulation processes. Moreover, there was a robust and

significant influence of distractor events on behaviour, suggesting that attention does not

fully attenuate irrelevant inputs. Overall, the results are consistent with a view that

attentional selection and evidence accumulation take place concurrently, with attention

mediating sensory processing and decision-making.

In Experiment 1, we used an increase in colour saturation to gradually reveal to

participants the task-relevance of the overlapping motion stimuli, and to render the

coherent motion signals discernible. While this design was clearly effective for measuring

the impact of distractors on decision making, is possible that attentional filtering of

distractors might have been more successful if participants had been given an opportunity

to fully select the task-relevant stimuli (cued target colour) prior to the onset of coherent

motion events. To test this hypothesis, in Experiment 2 the trial epochs were structured so

that the colours of the dot stimuli reached full saturation prior to the onset of coherent

motion events, thus effectively separating selection-related and decision-related signals in

time. Specifically, in Experiment 2 a new group of 36 participants viewed displays in which

the saturation of the target and distractor dots was initially ramped to maximum within

each epoch of the trial. The coherent motion events were then presented for .5 s at a

jittered interval during the period of maximum saturation (see Fig. 3a).

**Figure 3. Schematic of the stimuli, task and the behavioural results in Experiment 2. a,** Example stimulus

sequence from a typical trial (above) together with the timing of colour saturation modulation and coherent-

motion onsets (below). Only target-present epochs were presented, and the increase in colour saturation and

onset of coherent motion were separated in time. Dot patches were frequency-tagged at 12 and 18 Hz

(counterbalanced across target and distractor stimuli). **b,** Group-level histograms (bars) of the error magnitude

together with the best-fitting mixture-distribution models (pink lines). **c,** Average decision weights showing the

contributions of each presented motion direction to the decision. Grey dots denote individual participants.

To independently monitor the brain's responses to target and distractor motion, the

two sets of dots were flickered at different frequencies (12 and 18 Hz). Using a similar

approach, studies on visual attention have shown (34,35) that when two differently-

coloured, spatially overlapping random-dot patches are presented, electrophysiological

responses to the task-relevant, target patch are stronger than those to concurrent distractor

stimuli. Unlike previous studies, the design of Experiment 2 enabled us to track attentional

deployment within a trial as a function of stimulus discriminability. Specifically, we were

able to independently characterise the brain's responses to target and distractor patches

prior to, during, and after the modulation of colour saturation. Since the flickering stimuli

permitted independent tracking of target and distractor signals, we removed no-target

epochs and presented only target-present epochs.

The behavioural results of Experiment 2 were strikingly similar to those of

Experiment 1. Initial analyses revealed no effect of repeating vs. changing the target colour

(all ts < 1), so all subsequent analyses used the average of the two. Response precision (Fig.

3b) was high and comparable between one- and two-target colour trials (K/FWHM =

7.96/48° and 7.37/50°, respectively, $F_{1,30}$ = 2.37, p = .134). Likewise, guessing rates were low

and virtually identical for one- and two-target colour trials (ca. 12%, F < 1). Analyses of

decision weights revealed that both target and distractor signals contributed to the average

motion-direction response in all conditions (all p < .001). The weights (Fig. 3c) for targets,

however, were seven times higher than those for distractors (.56/.01 and .08/.01,

respectively, $F_{1,30}$ = 1,845, p < .001, $\eta_p^2$ = .98). The serial order effect from Experiment 1 was

also replicated, with higher decision weights for the first epoch than for the second, both for

targets (.58/.01 vs. .54/.01, $t_{30}$ = 3.06, p = .004) and distractors (.09/.01 vs. .07/.01, $t_{30}$ = 3.32, p

= .002). Finally, there was no significant difference between one- and two-target colour

trials, either as a main effect or in combination with the other factors (all F ≤ 1.35, all p ≥

.254).

We next characterised the time-course of the CPP. The ERP topography (Fig. 4a) in

Experiment 2 was broadly consistent with that of Experiment 1, showing a central-medial

positivity. The time-course of the CPP (Fig. 4b) throughout the trial closely followed the

modulation of colour saturation, peaking sharply around .8 and 2.8 s and decaying quickly

thereafter. There was also a second modulation, broadly coinciding with the coherent

motion onsets (at around 1.5 and 3.5 s), which, due to the jittered timing of the motion

onsets, rose and fell more slowly than the colour-evoked components. As in Experiment 1,

the phasic modulation of the CPP suggests that several episodes of evidence accumulation

took place throughout a trial. A single accumulation episode would have yielded a sustained

component throughout the trial, which clearly was not the case.

**Figure 4. Topography and time course of the CPP component in Experiment 2. a,** Surface-Laplacian-filtered

EEG topography averaged across all conditions at the middle of peak colour saturation for both epochs. **b,** The

CPP component averaged across all experimental conditions for the total trial duration. **c**, Time-course of the

CPP time-locked to the onset of colour saturation (left panels), and to the onset of coherent motion (right

panels), shown separately per epoch and experimental condition. Note the difference in scale between panels.

Conventions as in Figure 2.

Analyses of the CPP (Fig. 4c) time-locked to the onset of colour modulation and

coherent motion, respectively, revealed a significant positive deflection in both cases.

Analyses of *colour-locked CPPs* for the first epoch relative to the second revealed a shorter

onset latency (220 vs. 231 ms, $F_{c(1,30)} = 5.04$, p = .032), a marginally steeper slope (17.57 vs.

13.34 μV/s, $F_{c(1,30)} = 3.23$, p = .083) and a higher peak amplitude (1.95 and 1.42 μV, $F_{c(1,30)} =$

6.40, p = .017). In the second epoch, dividing attention between two target colours yielded a

significantly higher peak amplitude for two- versus one-target colour trials (1.56 and 1.29

μV, respectively; $t_{c(1,30)} = 2.30$, p = .029) . Analyses of *motion-locked CPPs*, by contrast,

revealed no significant differences in onset latency (270 ms), slope (9.44 μV/s) or peak

amplitude (1.27 μV) between experimental conditions (all $F_c <= 1.44$, all ps >= .240). Overall,

the ERP analyses of Experiment 2 suggest that both selecting the task-relevant colour patch

(i.e., attentional allocation) and deciding on the motion direction (i.e., perceptual

discrimination) involve some degree of evidence accumulation. Further, as only the colour-

locked CPP differed between the first and second epoch, it appears that the serial order

effect observed in both Experiments 1 and 2 was more closely related to processing of

colours rather than processing of the motion signal itself.

To independently characterise the brain's response to target and distractor signals,

we next analysed the amplitude of SSVEP responses elicited by the frequency-tagged

motion stimuli. There was a strong (≈2 dB) frequency-specific response which peaked at the

Oz electrode over the occipital pole (Fig. 5a,b). Time-frequency analyses revealed that the

power of both target and distractor signals was significantly different from zero throughout

the trial (all $p_{FDR-corrected}$ < .05).  Moreover, the power was similar for target and distractor

patches prior to the increase in colour saturation in both the first and second epochs (Fig.

5c). This suggests that participants divided attention across both patches during periods in

which the two patches were indistinguishable.

**Figure 5. Time-course of target and distractor processing measured as SSVEP power in Experiment 2. a,**

Topography of the total power at 12 Hz and 18 Hz normalized relative to the neighbouring frequencies,

computed using a fast-Fourier transform during periods of maximal colour saturation (.5–1.5 s, and 2.5–3.5 s).

**b,** Normalized total SSVEP power (M ± 95% CI) at Oz electrode during the period of maximal colour saturation

averaged across epochs and all experimental conditions. **c**, Time-resolved target- and distractor-evoked

SSVEPs for the whole trial duration averaged across all experimental conditions (M ± 1 within-participants

SEM). Black symbols above the x-axis denote times at which the difference between target and distractor

power was significant at $p_{FDR-corrected}$ < .05. **d**, Target-evoked (upper panels) and distractor-evoked (lower

panels) SSVEPs per epoch and per experimental condition baseline-corrected relative to .1 s interval around

the onset of maximum colour saturation (.5 and 2.5 s for the first and second epoch, respectively). Black

symbols above the x-axis denote times at which the baseline-corrected power was significantly different from

zero at $p_{FDR}$ < .05.

As the colour saturation increased, there was a transient *decrease* in power for the

two patches in both the first epoch (around .5 s) and the second (around 2.5 s). Whereas

the power for target patches in both epochs recovered quickly (Fig. 5d, upper panels), the

power for distractor patches remained unchanged throughout the epochs (Fig. 5d, lower

panels), yielding a robust effect of task-relevance (average power: .24 and .10 dB for target

and distractor patches, respectively, $F_{1,30}$ = 11.64, p = .002, $\eta_p^2$ = .28). Finally, the SSVEP power

was comparable across the first and second epochs, and across one- and two-target colours

(all F ≤ 1.25, all p ≥ .272). Taken together, the lower guessing rates and lower decision

weights in Experiment 2 relative to Experiment 1 suggest that preparation time improves

the selectivity of attentional filters. Nevertheless, both the decision weights and the SSVEPs

revealed that distractor signals still evoked brain responses and influenced participants'

average motion-direction decisions. In line with Experiment 1, the results of Experiment 2

suggest that selective attention cannot fully prevent task-irrelevant inputs from influencing

evidence accumulation.

*Discussion*

The goal of the present study was to characterise the behavioural and neural

processes associated with making integrated perceptual decisions. Unlike simple perceptual

decision-making (1,2,36), which requires judgments on a single, task-relevant stimulus, our

decision-making task involved selective processing of target signals in the presence of

distractors, and required integration of sensory evidence over an extended time period

within a trial. To characterise the role of selective attention in decision making, we used

mixture distribution modelling and regression analyses. To characterise the neural

correlates of decision-making, we used a widely accepted correlate of evidence

accumulation in humans, the centro-parietal positivity (CPP) component (3,11,20). Finally,

to monitor processing of different, task-relevant and task-irrelevant sensory inputs, in

Experiment 2 we flickered stimuli at different frequencies and measured SSVEPs to targets

and distractors.

The time-course of evidence accumulation, as indexed by CPP amplitude, co-varied

with the phasic modulation of colour saturation throughout each trial: the CPP was large at

high saturation levels and returned to baseline when the dots desaturated to grey. A single

evidence accumulation process would predict a sustained CPP response, whereas our

findings suggest that several episodes of evidence accumulation took place within a trial,

and these were triggered by the onset of task-relevant stimulus features. Experiment 2

revealed a strong CPP evoked by both colour and motion onsets (which were dissociated

within each trial), suggesting that the colour and motion signals engaged distinct evidence

accumulation processes in support of detecting a task-relevant colour, on the one hand, and

discriminating task-relevant motion signals, on the other. These findings are consistent with

studies which have used the evidence-accumulation framework to model behaviour in both

detection (13) and discrimination tasks (15).

The results of the two experiments suggest that selective attention operates as an

imperfect, real-time filter between perception and decision-making. Whereas targets had a

reliably stronger influence on behaviour and associated neural activity, distractor stimuli

also had a measurable influence on decision weights. In Experiment 1 there was a

measurable CPP in no-target epochs, suggesting that the onset of any sensory event within

a trial, whether target or distractor, triggered an episode of evidence accumulation.

Additionally, the robust and significant effect of no-target motion epochs on integrated

decisions suggests that participants were unable to suppress these distractor signals from

being accumulated. Taken together, the findings of Experiment 1 suggest that perceptual

decision making takes place in parallel with attentional selection. At early stages of

attentional selection, coherent motion information carried by both the target and distractor

patches are accumulated into the decision variable. As attentional selectivity increases, the

distractor inputs are attenuated, an observation that is consistent with the lower CPP

amplitude and lower decision weights for no-target epochs than target-present epochs.

Consistent with Experiment 1, the neural responses to distractors in Experiment 2, while

significantly smaller than those to targets, were not completely suppressed and remained

stable over the period during which target and distractor patches were discernible within

the trial. In Experiment 2, participants had ample time to select the task-relevant patch (> .5

s). Despite this, there was a robust distractor effect on responses suggesting that during

integrated decision-making tasks attention does not completely suppress the accumulation

of task-irrelevant sensory input.

353           Overall, the results of the present study are consistent with the notion that sensory

evidence accumulates in parallel (rather than sequentially) with increased selectivity for

task-relevant *features*. Computational modelling of response speed and accuracy in the

classic flanker task – in which target and distractor stimuli are presented concurrently at

different spatial locations (e.g., 37) – has shown that similar principles apply to selectivity

for task-relevant *locations* (15). Of note, in a recent study Wyart et al. (2015) had

participants report the average orientation of one of two spatially separated streams of

achromatic gratings. Unlike the present study, decision weights for the spatially separated

distractors were not statistically different from zero. While differences in experimental tasks

and analytical approaches prevent direct comparisons between our study and that of Wyart

et al. (2015), the two sets of findings suggest that space- and feature-based filtering of

sensory inputs during evidence accumulation may exhibit different properties. Specifically,

sensory evidence accumulation might be restricted to a finite region of space so that under

conditions in which signals are sufficiently separated they engage independent

accumulators.

368           Interestingly, across both experiments, having participants divide attention between

two potential target colours yielded no behavioural cost relative to having them focus on a

single target colour. In addition, there was no evidence of a cost for switching between

target colours across two epochs, compared with trials in which the two colours repeated.

Since in the present study the target colour patches were rendered increasingly visible over

a prolonged time interval and the responses were not speeded, it is possible that our

paradigm was insensitive to potential behavioural costs of dividing attention (but see, e.g.,

Eimer and Grubert, 2014; Grubert et al., 2017). On the other hand, the neural correlates of

decision making, as characterised by the onset latency, slope, and peak CPP amplitude,

were consistent with the behavioural findings: the CPP time-traces were virtually identical

for one- and two-target colour trials in both experiments. As the specifics of our

experimental design prevent any strong conclusions, these findings call for further

investigation.

In both experiments, we also found a significant serial order bias with higher

decision weights for the first target epoch relative to the second. Whereas, in Experiment 1,

higher target weights were accompanied by lower distractor weights, in Experiment 2 the

weights for both target and distractor signals were higher in the first than the second epoch.

This primacy effect was not expected and, in fact, studies using similar paradigms typically

reported either no order effects or even the opposite, recency effects (16,40,41). Mirroring

the behavioural primacy effects, the colour-locked peak CPP amplitude was higher for the

first than the second epoch. By contrast, analyses of the motion-locked CPP in Experiment 2

revealed no order effects. These results suggest that the primacy effects might be related to

processing colours rather than motion. Since previous studies did not modulate attention-

related signals in the way we did here, the primacy effects we observed are not necessarily

inconsistent with the literature. Further studies will be necessary to characterise this effect

in more detail.

The motion averaging task we have introduced here has potential as a tool for

investigating the mechanisms underlying more complex, integrated decision-making.

Dynamic weighting of individual decisions to inform a single, integrated decision is

ubiquitous in daily life: for example, when deciding whether or not to cross a busy road. In

our task, individual motion signals are uncorrelated and, considered in isolation, are not

predictive of the final decision. Hence, the averaging task permits independent

parameterisation of both *simple* and *integrative* decision-making processes in a

straightforward and well characterised motion discrimination task. Using neuroimaging

methods with high spatial resolution such as fMRI, future studies could identify the brain

areas involved in simple decision-making, on the one hand, and integrative decision-making,

on the other. Using this task to characterise decision-making across the lifespan or in clinical

groups could shed light on the development of integrative decision-making abilities which

are a hallmark of adaptive, intelligent behaviour.

*Materials and Methods*

**Participants.** Seventy-two healthy volunteers (39 females, average age 21.5 ± 2.5

years, 36 per experiment) participated in the study after providing written informed

consent. All had normal or corrected-to-normal visual acuity and normal colour vision. In

Experiment 1, three participants were identified as outliers based on their behavioural

performance and/or EEG signals (see below for details). Data from five participants were

removed from Experiment 2, based on the same criteria, leaving 33 and 31 participants per

experiment, respectively. The study was approved by the Human Research Ethics

Committee of The University of Queensland (approval nr. 2016001247), and was conducted

in accordance with the Human Subjects Guidelines of the Declaration of Helsinki.

**Stimuli, task and procedure.** In Experiment 1, participants were asked to monitor

*three* successively presented epochs of coherent motion within each trial, and to indicate

the average direction of *two* target-motion events at the end of the trial using a response

dial. A response feedback symbol showing the correct answer was presented after every

trial.

At the beginning of each trial, a central disk cued participants to the target colour to

monitor for during the upcoming trial (Fig. 1a). Different colours were counterbalanced

across participants. The cue was followed by a buffer period showing a field of 80 grey,

randomly-moving dots. The dots' colour saturation gradually increased before returning to

grey (Fig. 1b). The increase in saturation revealed two overlapping, coloured-dot patches

moving in different directions. Each trial consisted of three epochs – in two of these epochs

one dot patch was rendered in the target colour, and the other appeared in a distractor

colour. Target patches were displayed equally often in the first, second and third epochs of

a trial. In the remaining (no target/distractor only) epoch, neither of the patches had a

target colour.

To characterise potential effects of the number of task-relevant colours to be

monitored, in separate blocks of trials participants were cued to look for either one target

colour (e.g., blue), or two different target colours (e.g., blue and yellow). In two target-

colour trials, there was an equal numbers of trials in which the target colour repeated or

changed between two target-present epochs within the trial. For each participant, distractor

colours were always different from target colours. Combinations of target and distractor

colours were counterbalanced across participants.

Dot-motion was generated at a suprathreshold level (40% coherence), with a speed

of 19°/s, 100 ms dot-life, and with different signal-dots across frames and random-walk

noise-dots (23). Although coherent motion was present throughout the epoch (1.5 s, Fig.

1b), different motion directions were discernible only at higher colour saturations. The

motion directions were uniformly sampled from 0°–359°, with the target-distractor and

target-target difference remaining within 30°–150°. Five easily distinguishable colours (Fig.

1b) were selected in the HSL colour-space with a minimum hue difference of 72° and

medium saturation and brightness (50). Two randomly-selected colours served as targets

and two as distractors. Participants completed 30 practice trials followed by six blocks of 44

trials (264 trials in total). Each experimental session lasted approximately one hour.

In Experiment 2, to measure responses to targets and distractors independently, the

dot fields corresponding to target and distractor signals flickered (ON-OFF) concurrently at

different frequencies (12 and 18 Hz). The pairing between a given frequency and stimulus

type (target vs. distractor) was counterbalanced across trials. The introduction of these

flickering displays yielded distinct, time-resolved steady-state evoked potentials (SSVEPs,

see Norcia *et al.*, 2015), which enabled us to read out the strength of target and distractor

representations on each trial. To optimise the display for recording SSVEPs, the field size,

dot size and dot number were doubled in Experiment 2 (Fig. 3a) relative to Experiment 1.

The dot-motion was generated at 2.5°/s, with an infinite dot life. Three distinctive colours

(maximum saturation 75, minimum colour separation 90°, Fig. 3a) were selected; two

colours served as targets, and the remaining one served as a distractor. The distractor and

target colours were counterbalanced across participants. The colour saturation increased

rapidly (.25 s) from grey to full saturation, and remained at maximum saturation for 1 s. In

contrast to Experiment 1, in which three epochs of coloured dots were shown, in

Experiment 2 only two epochs of dots were shown, and both epochs within a trial contained

a target-motion patch (i.e., there was no longer a no target/distractor only epoch). Coherent

motion events were presented for .5 s during the maximum saturation period, and at

variable times (.50–.75 s asynchrony relative to the onset of colour modulation).

Participants completed 64 practice trials followed by six blocks of 64 trials (384 trials in

total). All other details were the same as in Experiment 1.

**Apparatus.** The experiments were conducted in a dark, acoustically and

electromagnetically shielded room. The stimuli were presented on a 24" monitor with

1920×1080 resolution and a refresh rate of 144 Hz. The experimental software was custom-

coded in Python using the PsychoPy (25,26) toolbox. EEG signals were recorded using 64 Ag-

AgCl electrodes (BioSemi ActiveTwo) arranged in the 10-20 layout, and sampled at 1,024 Hz.

**Behavioural analyses.** To identify outlier participants, the distributions of error

magnitudes (i.e., the angular difference between the response and the correct answer)

were compared to a uniform distribution (i.e., pure guessing) using the Kolmogorov-Smirnov

test. Participants for whom the probability of the null hypothesis (i.e., a uniform distribution

of error magnitudes) exceeded .001 were removed from further analyses. The remaining

distributions per experimental condition and per participant were fitted to a theoretical

model (27), and responses were separated into noisy target responses and random guesses.

To quantify decision weights, a multiple-regression (OLS) model with a term for each of the

presented motion directions, expressed as complex numbers, was fitted to the responses,

separately per participant and experimental condition. The absolute value of the resulting

regression coefficients reflects the influence of each of the presented coherent motion

signals on the response, i.e., its *decision weight*. As the decision weights were always

positive, we used permutation test (10,000 permutations) to generate the empirical null

distribution against which the empirical decision weights were tested.

**EEG analyses.** EEG signals were analysed using the MNE-Python (28) toolbox. The

data were offline re-referenced to the average electrode, low-pass filtered at 99 Hz and

notch-filtered at 50 Hz to eliminate line noise. The recorded signal was pre-processed using

the FASTER (29) algorithm for automated artefact rejection. The pre-processed signal was

down-sampled to 256 Hz, segmented into epochs between the cue-onset and the response-

display onset, baseline-corrected relative to -.1–0 s pre-trial and linearly de-trended. Outlier

epochs and participants were identified using the FASTER algorithm and removed from

further analyses.

To characterise the temporal dynamics of evidence accumulation, we quantified the

onset latency, slope and peak amplitude of an ERP known as the central-parietal positivity

(CPP). Previous research has shown that the time-course of the CPP closely resembles the

time-course of evidence accumulation: specifically, its amplitude builds up gradually (8), the

build-up slope is proportional to stimulus quality (9), and it is observed even in the absence

of overt responses (10). The CPP ERP was computed by averaging Cz/CPz electrodes across

trials. Each epoch within a trial was extracted from the onset of the increase in colour

saturation and baseline-corrected relative to a common baseline during -.1–0 s, averaged

across all epochs. The peak CPP amplitudes were identified using the jackknife-method (30).

Using the same method, ERP onset latencies were computed at 50% peak amplitude. The

ERP slopes were computed as the amplitude difference between -.05 s and .05 s relative to

the ERP onset, and divided by .1 s so as to yield μV/s.

Time-resolved SSVEP power at tagged frequencies was computed using Morlet

wavelets with fixed-width .5 s Gaussian taper, and normalized relative to the neighbouring

frequencies. The mean power per epoch was computed during the 1 s of maximal colour

saturation. For analyses of the target and distractor SSVEPs, the power per epoch was

baseline-corrected relative to a .1 s interval around the onset of maximal colour saturation

(.5 and 2.5 s, for the first and the second epochs, respectively).

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