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The Role of Object Individuation in Attention and Visual Processing

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Turner Institute for Brain and Mental Health, School of Psychological Sciences, Monash University, Clayton, 3800 Victoria, Australia Review of Foster et al.

Throughout daily life, we are exposed to excess information that is beyond our capacity to process. Selective attention filters out unnecessary noise and allows us to focus on relevant stimuli (Noonan et al., 2018). Research has long focused on trying to uncover the complex neural mechanisms that underlie attention and its role in perception and, consequently, decision-making. Extensive behavioral data have consistently shown, for example, that cuing the location of an upcoming target leads to more accurate and faster responses, suggesting that covert attention increases the rate of processing for visual stimuli at the attended location (Carrasco and McElree, 2001; Carrasco et al., 2006; Grubb et al., 2015). What remains unclear, however, is exactly how covert attention exerts this influence: is it via enhancement of early sensory processing, via enhanced integration of sensory input (i.e., evidence accumulation), or via response preparation?

Research has established several neurophysiological markers that may represent different aspects of attention and visual processing. For example, in electroencephalographic (EEG) recordings, an early negative voltage deflection occurs $\sim\!150-300$ ms after target presentation and is

measured at lateralized temporal occipital sites. This voltage deflection is termed the "N2pc" and has frequently been the subject of investigation in attention studies. Although widely believed to be involved in early selection processes, the mechanism underlying the N2pc is still debated (Hickey et al., 2006; Kiss et al., 2008; Mazza and Caramazza, 2015). One line of research has proposed that the N2pc reflects attention selection related to object individuation (Kiss et al., 2008); that is, the transformation of raw sensory information into an object (target) representation (Mazza and Caramazza, 2015). Consistent with this view, studies have shown that N2pc amplitude is influenced by the number of items that need to be individuated (Pagano and Mazza, 2012), whereas no such effect is observed when individuation is not required (Mazza and Caramazza, 2011).

To understand how covert attention influences visual processing, Foster et al. (2020) recorded EEG continuously while subjects performed a visual search task. They measured differences in the latency of the N2pc instead of amplitude, because previous research that focused on amplitude effects has been unable to fully explain behavioral effects (Di Russo et al., 2003). Additionally, research on latency effects has been inconclusive. Because of previous research suggesting that the N2pc may reflect shifts of attention rather than object individuation (Eimer, 1996), Foster et al. (2020) attempted to exclude this explanation to provide stronger support for the object individuation account. They implemented an inverted encoding model with alpha-band activity used to track the allocation of spatial attention. Inverted encoding models allow one to estimate specific aspects of neuronal activity from recordings of population activity. For example, a signal reflecting the subpopulation of neurons tuned for a specific visual stimulus property, such as spatial location, might be estimated from alpha-band activity in the EEG (Foster et al., 2017; Liu et al., 2018). Foster et al. (2020) modeled alpha activity at each electrode as a weighted sum of eight channels tuned for eight possible stimulus locations. As a result of this model inversion process, they were able to use alpha-band activity to track endogenous allocation of spatial attention over time. If participants allocated attention to the cued target location before target onset, and not after target onset, then any target-elicited N2pc effects would therefore represent another mechanism, such as object individuation.

Across two experiments, participants searched for a target shape, a diamond with a missing corner, among a series of seven distractor squares. Participants had to report which side of the target (left/ right) was missing a corner. Participants were instructed that half of the trials were preceded by a cue revealing the exact location of the upcoming target (informative cues), and half were preceded by a cue revealing no information (noninformative cues). Consistent with previous research, the participants showed increased accu-

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racy and faster reaction times with informative cues than with noninformative cues, suggesting covert attention was speeding visual processing.

Foster et al. (2020) also observed earlier (by \sim 22 ms) N2pc onsets for informative cues than for noninformative cues. This is a key finding, as it is the first evidence of covert attention affecting the latency of an EEG marker and indicates that covert attention speeds visual processing by affecting the N2pc. Additionally, the alphaband analyses revealed that participants attended to the cued target location before target onset during informative cue conditions, but did not allocate attention when given noninformative cues. This suggests that the effects observed for the N2pc were unlikely to reflect shifting attention, as this was not required after target onset. The authors conclude that these results provide support for the object individuation account of the N2pc and suggest that covert attention speeds visual processing through this process.

The results presented by Foster et al. (2020) have important implications for how we understand the role of covert attention in visual processing and subsequent influences on behavior. Here they show that covert attention influences N2pc latency, and with their alpha-band power analyses they provide support for an object individuation interpretation of the N2pc. This suggests that the well established finding that induced covert attention speeds visual processing (Carrasco and McElree, 2001; Carrasco et al., 2006; Grubb et al., 2015) occurs via speeding the process of object individuation. However, it is important to consider broader interpretations of the results and ask whether further analyses could clarify these results and lead to further insight into the role of covert attention in visual processing.

A related area of research has focused on understanding the relationship between distractor suppression and target enhancement in selective attention. Previous research has suggested that these are independent processes and may be achieved by separate mechanisms (Wöstmann et al., 2019). Moreover, there has been debate about whether the N2pc reflects mainly distractor suppression (Luck and Hillyard, 1994) or enhancement of target-processing mechanisms (Eimer, 1996; Hickey et al., 2009; Mazza et al., 2009; Loughnane et al., 2016). The object individuation interpretation strongly aligns with the target enhancement account; it describes the process facilitating the binding of features to form a representation of the target object and has been proposed in opposition to the distractor suppression account (Mazza et al., 2009; Mazza and Caramazza, 2015). The data presented by Foster et al. (2020) do not completely exclude a distractor suppression explanation, however. For example, given that participants precisely attended to the target location before target onset, they may have been more prepared to suppress distractors. Consequently, such suppression would occur earlier, and thus could explain the earlier N2pc observed under informative cue conditions.

It is also important to consider that the N2pc may reflect a complex interaction of mechanisms involved in attention. The N2pc is a composite waveform. It is measured by subtracting the negative waveform observed at sites ipsilateral to target location (N2i) from the negative waveform observed at contralateral sites (N2c). By using the N2pc, the authors may have masked independent, lateralized effects (Hickey et al., 2006). Recent research has focused on the N2c and N2i separately (Loughnane et al., 2016; Newman et al., 2017). This line of research supports the notion that the N2i and N2c are independent EEG components reflecting different mechanisms. Loughnane et al. (2016), for example, showed that N2c amplitude predicted reaction time through its influence on the onset and buildup rate of the centroparietal positivity (CPP), a neuronal marker of evidence accumulation (O'Connell et al., 2012; Loughnane et al., 2016; Newman et al., 2017). Similarly, Newman et al. (2017) found a relationship between pretarget alpha power, N2c latency, and the CPP that explained visuospatial bias observed in individuals. Although the N2i is influenced by target salience, it has not yet been shown to have a clear relationship with behavior (Loughnane et al., 2016; Newman et al., 2017). Nonetheless, this demonstrates that the two signals may reflect independent mechanisms. Therefore, examining the lateralized effects of covert attention in the paradigm used by Foster et al. (2020) may help us understand the relative contribution of target enhancement/object individuation and distractor suppression on these waveforms.

Further investigation of the relationship between the N2 signals and other markers of visual processing may also aid in our interpretation of the behavioral results observed by Foster et al. (2020). As the authors discuss, the informative cue conditions resulted in reaction times \sim 50 ms earlier than the noninformative condition. Given that the latency effects of the N2pc are \sim 20 ms, this suggests there may be more involved in this process than what is reflected by just the N2pc. Indeed, the authors mention that effects on earlier sensory representation and/or later decision or response preparation are possible. Considering this, it would be valuable to explore how the latency effect may relate to other stages of visual processing and subsequent decision-making, and to what degree this can explain behavior.

Previous research has identified relationships between alpha power measures and N2pc/N2 signals that appear to influence behavior (Newman et al., 2017; Bacigalupo and Luck, 2019). Newman et al. (2017), for example, showed that greater suppression of pretarget alpha power in the right hemisphere predicted earlier N2c onsets for left hemifield targets, which further influenced a marker of evidence accumulation and reaction time. Additionally, Bacigalupo and Luck (2019) showed in a visual search task that the suppression of alpha power in posterior regions in response to the presentation of the target may have an active role in target processing and may reflect a related, yet separate, mechanism to the N2pc. Further investigation of the relationship between alpha power and N2pc/N2 signals may help to further explain the reaction time results observed by Foster et al. (2020). For example, does asymmetry in pretarget alpha suppression predict N2 signal latency and/or response time? Is this relationship modulated by cueing target location? Would the magnitude of targetelicited alpha power suppression also be influenced by covert attention? Exploring these possibilities may better explain the response time differences observed.

To conclude, Foster et al. (2020) offer novel findings about the role of covert attention in visual processing by showing that it speeds the onset of the N2pc and providing compelling evidence that this reflects object individuation. This finding will be an asset to future research that continues to break down the role of covert attention in visual processing, which may aid our understanding of why and how these systems fail.

References

- Bacigalupo F, Luck SJ (2019) Lateralized suppression of alpha-band EEG activity as a mechanism of target processing. J Neurosci 39:900– 917.
- Carrasco M, McElree B (2001) Covert attention accelerates the rate of visual information

processing. Proc Natl Acad Sci U S A 98:5363–5367.

- Carrasco M, Giordano AM, McElree B (2006) Attention speeds processing across eccentricity: feature and conjunction searches. Vision Res 46:2028–2040.
- Di Russo F, Martínez A, Hillyard SA (2003) Source analysis of event-related cortical activity during visuo-spatial attention. Cereb Cortex 13:486– 499.
- Eimer M (1996) The N2pc component as an indicator of attentional selectivity. Electroencephalogr Clin Neurophysiol 99:225–234.
- Foster JJ, Sutterer DW, Serences JT, Vogel EK, Awh E (2017) Alpha-band oscillations enable spatially and temporally resolved tracking of covert spatial attention. Psychol Sci 28:929– 941.
- Foster JJ, Bsales EM, Awh E (2020) Covert spatial attention speeds target individuation. J Neurosci 40:2717–2726.
- Grubb MA, White AL, Heeger DJ, Carrasco M (2015) Interactions between voluntary and involuntary attention modulate the quality and temporal dynamics of visual processing. Psychon Bull Rev 22:437–444.

- Hickey C, McDonald JJ, Theeuwes J (2006) Electrophysiological evidence of the capture of visual attention. J Cogn Neurosci 18:604–613.
- Hickey C, Di Lollo V, McDonald JJ (2009) Electrophysiological indices of target and distractor processing in visual search. J Cogn Neurosci 21:760–775.
- Kiss M, Van Velzen J, Eimer M (2008) The N2pc component and its links to attention shifts and spatially selective visual processing. Psychophysiology 45:240–249.
- Liu T, Cable D, Gardner JL (2018) Inverted encoding models of human population response conflate noise and neural tuning width. J Neurosci 38:398–408.
- Loughnane GM, Newman DP, Bellgrove MA, Lalor EC, Kelly SP, O'Connell RG (2016) Target selection signals influence perceptual decisions by modulating the onset and rate of evidence accumulation. Curr Biol 26:496–502.
- Luck SJ, Hillyard SA (1994) Spatial filtering during visual search: evidence from human electrophysiology. J Exp Psychol Hum Percept Perform 20:1000–1014.
- Mazza V, Caramazza A (2011) Temporal brain dynamics of multiple object processing: the flexibility of individuation. PLoS One 6:e17453.

- Mazza V, Caramazza A (2015) Multiple object individuation and subitizing in enumeration: a view from electrophysiology. Front Hum Neurosci 9:162.
- Mazza V, Turatto M, Caramazza A (2009) Attention selection, distractor suppression and N2pc. Cortex 45:879–890.
- Newman DP, Loughnane GM, Kelly SP, Connell RG, Bellgrove MA (2017) Visuospatial asymmetries arise from differences in the onset time of perceptual evidence accumulation. J Neurosci 37:3378–3385.
- Noonan MP, Crittenden BM, Jensen O, Stokes MG (2018) Selective inhibition of distracting input. Behav Brain Res 355:36–47.
- O'Connell RG, Dockree PM, Kelly SP (2012) A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. Nat Neurosci 15:1729–1735.
- Pagano S, Mazza V (2012) Individuation of multiple targets during visual enumeration: new insights from electrophysiology. Neuropsychologia 50:754–761.
- Wöstmann M, Alavash M, Obleser J (2019) Alpha oscillations in the human brain implement distractor suppression independent of target selection. J Neurosci 39:9797–9805.