



The neural systems for perceptual updating

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ABSTRACT

In a constantly changing environment we must adapt to both abrupt and gradual changes to incoming information. Previously, we demonstrated that a distributed network (including the anterior insula and anterior cingulate cortex) was active when participants updated their initial representations (e.g., it's a cat) in a gradually morphing picture task (e.g., now it's a rabbit; Stöttinger et al., 2015). To shed light on whether these activations reflect the proactive decisions to update or perceptual uncertainty, we introduced two additional conditions. By presenting picture morphs twice we controlled for uncertainty in perceptual decision making. Inducing an abrupt shift in a third condition allowed us to differentiate between a proactive decision in uncertainty-driven updating and a reactive decision in surprise-based updating. We replicated our earlier result, showing the robustness of the effect. In addition, we found activation in the anterior insula (bilaterally) and the mid frontal area/ACC in all three conditions, indicative of the importance of these areas in updating of all kinds. When participants were naïve as to the identity of the second object, we found higher activations in the mid-cingulate cortex and cuneus – areas typically associated with task difficulty, in addition to higher activations in the right TPJ most likely reflecting the shift to a new perspective. Activations associated with the proactive decision to update to a new interpretation were found in a network including the dorsal ACC known to be involved in exploration and the endogenous decision to switch to a new interpretation. These findings suggest a general network commonly engaged in all types of perceptual decision making supported by additional networks associated with perceptual uncertainty or updating provoked by either proactive or reactive decision making.

1. Introduction

Every day we are confronted with an enormous amount of information. Mental models compress incoming sensory information into a tractable form to optimally guide decision making (Johnson-Laird, 2004; Tenenbaum et al., 2011). We rely on such representations for a wide range of decisions. However, the world is in constant flux. In order for our mental models to be useful we must be capable of revising them in the face of environmental changes. While sometimes the decision to update to a new interpretation (e.g., Is this food edible or not?) is accompanied by a certain degree of uncertainty (e.g., When is my steak grilled to perfection?). At other times this decision is made for us and we only have to react to the changes in the environment (e.g., the steak falls from the barbecue; McGuire et al., 2014).

We previously demonstrated that a distributed network including the anterior insula, dorso-medial prefrontal cortex, and inferior parietal lobes was activated when participants updated their representations to the gradual accumulation of changing information (Stöttinger et al.,

2015). Participants viewed picture sets in which one unique object (e.g., a shark) morphed slowly over fifteen iterations into a completely different unique object (e.g., a plane). Participants pressed different buttons to indicate whether they saw the first or another object. The average amount of change (in pixels) between each transition was held constant at ~ 4% with no significant difference between the individual picture positions (Stöttinger et al., 2016). Consequently, the transition from an old to a new model was internally determined by the individual as opposed to being driven by external events. The highest activations were found in the anterior insula (bilaterally) and mid frontal area including the anterior cingulate cortex (ACC). These areas were not only active at the time point of change but also immediately before, suggesting a possible causal role of these areas in updating. This finding was consistent with earlier results in patients showing that damage to the anterior insula – especially on the right – resulted in selective updating impairments in both the picture morphing task and in playing a simple competitive game (Danckert et al., 2012; Stöttinger et al., 2014; under revision), indicating a general updating impairment across

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different cognitive domains.

The results could be explained in three ways. First, activations may reflect *proactive decisions* to update, based on imprecision of the initial belief (McGuire et al., 2014): Given that differences between pictures were held constant with no abrupt deviations, it was up to the participant to decide at which point their initial representation was no longer supported by the evidence from the environment. This is similar to bistable perception where participants report which of two interpretations of an object they hold, despite no environmental change in the stimulus. The anterior insula is active when participants switch between interpretations of such stimuli (Lumer and Rees, 1999; Knapen et al., 2011; Müller et al., 2005; Weilhhammer et al., 2017). Despite the difference between spontaneous alternations in bistable perception and updating based on actual, albeit subtle, changes – a similar mechanism may be involved. In both cases the transition from the old to the new interpretation is determined internally by the participant rather than being determined by events in the environment. A second way to explain our prior results is via *perceptual uncertainty*: While all picture sets were based on the prerequisite that they were perceived categorically in our normative study (Stöttinger et al., 2016), we cannot fully rule out that decisions were accompanied by a certain degree of perceptual uncertainty. This would fit with research showing that a network including the anterior insula is engaged when belief updating is based on relative uncertainty in a gradually changing, noisy, uncertain, or perceptually degraded environment (Ploran et al., 2007; Heekeren et al., 2008 for review). Similarly, activation in the insula is modulated by the ambiguity of sensory information (Lamichhane et al., 2016; Sterzer and Kleinschmidt, 2010 for a review). A third potential explanation of our results would suggest that activations reflected a more general network always active whenever we update mental representations. This is in line with research on surprise-based updating which assigns a central role to the anterior insula and ACC. When observations in our environment saliently deviate from expectations, the right anterior insula initiates attentional control by activating the central executive network and deactivating the default mode network. As a consequence, cognitive resources are assigned to facilitate processing of the surprising, salient stimulus. The co-activation with the ACC allows rapid access to the motor system (Craig, 2009; Menon and Uddin, 2010; Uddin, 2015 for a review). The network found in our study might therefore be best understood more generally as a network for updating mental representations, signaled either by bottom-up salience, or internal signals.

The aim of this research was to evaluate each of these three explanations. That is, which brain areas are active regardless of the mechanism involved (proactive decision vs. perceptual uncertainty) and which brain areas are specific to each process. We presented participants with three different conditions: (1) *gradual-naïve condition*: In 10 separate sets pictures morphed gradually from one object to a second – replicating our initial study (Stöttinger et al., 2015). (2) A *gradual-repeat condition*: where all gradually morphing sets were presented twice thus diminishing perceptual uncertainty. For both series continuous changes result in the proactive decision to update a perceptual model due to the gradual accumulation of evidence. In the gradual-naïve condition the decision is accompanied by a greater degree of uncertainty, given the participant does not know what the second object will be. This uncertainty is reduced when the participant is exposed to this same set a second time (the gradual-repeat condition). As a further control for neural systems responding *reactively* to change we added an (3) *abrupt condition* where after a certain number of subtly changing pictures (akin to the gradual-naïve condition) updating was provoked by a dramatic change in the external input by switching to a new picture that was not coherent with the current pictorial set. Participants in the abrupt condition simply had to *react* to the abrupt change in visual input while updating in the gradual-naïve condition required them to *proactively decide* at which point their initial model was no longer supported by the evidence.

We first replicated our previous results. We then evaluated which

activations were associated with a switch in general, irrespective of an active decision to update to a new model or perceptual uncertainty. Finally, by comparing brain activation associated with a shift in conscious percept in the gradual-naïve condition with activations for the same shift in the abrupt condition we identified areas selectively associated with proactive decisions. In a similar vein, comparing perceptual shifts in the gradual-naïve condition with shifts in the gradual repeat condition allowed us to evaluate the influence of perceptual uncertainty.

2. Methods

2.1. Participants

A total of twenty (11 female) neurologically healthy participants with normal or corrected to normal vision took part in this study for payment. Due to a technical problem, data of one participant could not be analyzed. The final sample comprised nineteen participants (10 female; mean age 24.55 years, SD = 4.02). One participant reported being left-hand dominant. The individual activation pattern of this participant did not deviate from the activation pattern of the right-hand-dominant group. Given that left-handed people represent a portion of the population we decided to include this participant in the sample (see Willems et al., 2014 for that argument). None of the participants had a history of brain injury. All participants provided informed consent prior to participation. The research protocol was approved by the Office of Research Ethics at the University of Waterloo and the Tri-Hospital Research Ethics Board of the Region of Waterloo in Ontario, Canada.

2.2. The picture morphing task

2.2.1. Stimuli

Each participant saw thirty picture sets selected from a larger set validated in an earlier study (Stöttinger et al., 2016; <https://osf.io/qi2vg/>). All pictures were silhouettes of line drawings and of a standard size (316 × 316 pixels) – displayed on a white background (Fig. 1). All participants saw three different types of picture sets: (1) Gradual-naïve condition: In ten picture sets line drawings of common objects morphed over fifteen iterations into a different object (a replication of Stöttinger et al., 2015). (2) Gradual-Repeat condition: all gradually morphing sets were presented a second time. (3) Abrupt condition: In ten picture sets a salient switch was induced after the 4th, 5th, 6th, 7th, or 8th position (there were two sets for each switch position and switch position was randomly assigned across the six runs with the constraint that the same switch position did not occur within the same run). This switch violated the continuous changes used in the first two conditions in that the change was to an image from an unrelated set (Fig. 1, bottom line). Please note that picture sets used in the abrupt condition were different from the sets used in the continuous conditions. In order to keep the abrupt condition as similar as possible to the gradual-naïve condition, the first three pictures of a set were repeated. This resulted in subtle changes between pictures – similar to the ones in the gradual-naïve condition. Data from a pilot study suggested that participants typically do not notice this level of repetition: No participant reported noticing the repetition and reaction times reliably ramped up before the switch in all conditions. This suggests that participants were actively looking for the second object given that they did not know whether they were in the gradual-naïve or abrupt condition. Repeating the first three pictures in the abrupt condition had the advantage that picture sets were comparable in both conditions while guaranteeing that participants did not shift to a new interpretation before the intended change point.

Of the sixty pictures used, thirty-one depicted an animate object (e.g., animal) and twenty-nine displayed an inanimate object. In ten sets the object morphed from an animate object into a different animate object (e.g., cat – owl), in nine cases the object morphed within the inanimacy class (e.g., key – saw). In six picture sets the object morphed

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