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The eyes anticipate where objects will move based on their shape

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Imagine staring into a clear river, starving, desperately searching for a fish to spear and cook. You see a dark shape lurking beneath the surface. It doesn't resemble any sort of fish you've encountered before — but you're hungry. To catch it, you need to anticipate which way it will move when you lunge for it, to compensate for your own sensory and motor processing delays[1–3]. Yet you know nothing about the behaviour of this creature, and do not know in which direction it will try to escape. What cues do you then use to drive such anticipatory responses? Fortunately, many species[4], including humans, have the remarkable ability to predict the directionality of objects based on their shape — even if they are unfamiliar and so we cannot rely on semantic knowledge about their movements[5]. While it is known that such directional inferences can guide attention[5], we do not yet fully understand how such causal inferences are made, or the extent to which they enable anticipatory behaviours. Does the oculomotor system, which moves our eyes to optimise visual input, use directional inferences from shape to anticipate upcoming motion direction? Such anticipation is necessary to stabilise the moving object on the high-resolution fovea of the retina while tracking the shape, a primary goal of the oculomotor system[6], and to guide any future interactions[7,8]. Here, we leveraged a well-known behaviour of the oculomotor system: anticipatory smooth eye movements (ASEM), where an increase in eye velocity is observed in the direction of a stimulus' expected motion, *before* the stimulus actually moves[3], to show that the oculomotor system extracts directional information from shape, and uses this inference to predict and anticipate upcoming motion.

To test this, we first measured the perceived directionality of 64 shapes, each presented at four different orientations (total 256 shapes). Online participants (N = 336) rated the direction they thought the shape would be most likely to move[5] (Figure 1A). We selected 100 shapes with the strongest directional ratings as measured by the mean resultant length of participant responses (as measured by the mean resultant length of participant responses; see Supplemental information) for use in an ASEM experiment (Figure 1B). Here, participants (N = 14 for each experiment) fixated a static shape in the centre of the screen for 500 ms, after which the stimulus disappeared for 400 ms, and reappeared moving at a constant velocity of 10 deg/s in a direction either congruent with its perceived directionality (congruent condition, Experiments 1 and 2), or incongruent to its perceived directionality (incongruent condition, Experiment 2). We compared the average eye velocity around the time of stimulus onset (ASEM index; –50 ms before stimulus onset to +50 ms after stimulus onset divided by target velocity[3]) between directional shapes versus a non-informative circle. For Experiment 1 (Figure 1C), eye velocity was higher at the time of stimulus onset for directional shapes versus circles ($t(13) = 5.92$, $p < 0.0001$), indicating an anticipatory response to the directional cues provided by the shapes. The magnitude of the ASEM index increased as the strength of the shape's perceived directionality also increased (Figure 1D; $F(3,52) = 3.5$, $p = 0.022$).

This result was replicated in Experiment 2, with the additional

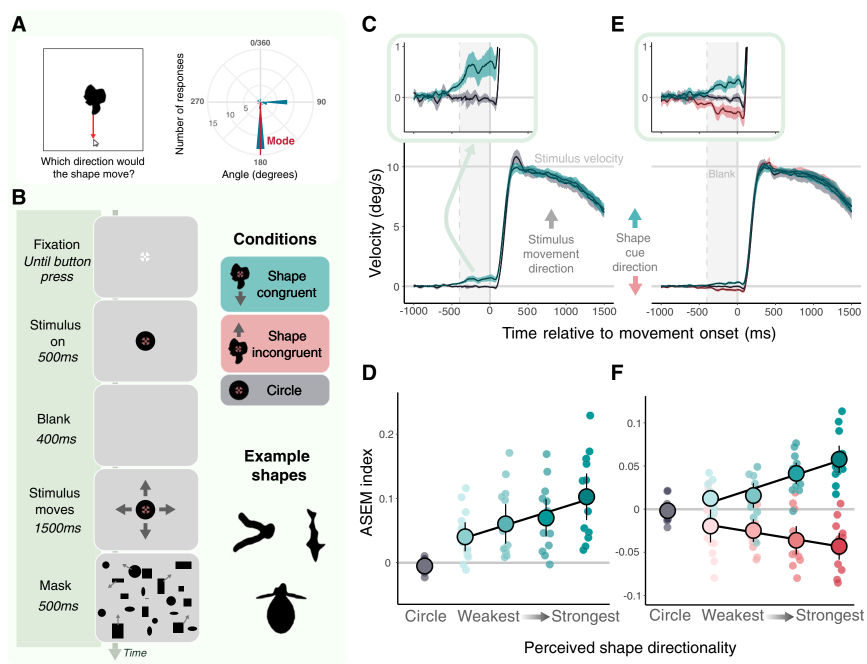

Figure 1. In an anticipatory smooth eye movement paradigm, anticipatory eye velocity increased with the strength of the perceived directionality of a shape.
(A) In a preliminary online experiment, participants indicated the direction they perceived a shape would move. (B) We used these directionality ratings in a subsequent lab-based eye-tracking experiment, where participants saw a shape (directional shape or circle) for 500 ms. After a 400 ms gap, the stimulus moved in a direction either congruent (Experiments 1 and 2) or incongruent (Experiment 2) with the perceived direction of the shape. (C,E) Mean velocity traces for congruent shapes (green), incongruent shapes (red) and circles (grey) relative to stimulus onset (0 ms). (D,F) ASEM index (average velocity ± 50 ms relative to stimulus onset divided by target velocity) for circles, and for shapes grouped by the strength of agreement in directionality ratings of individual shapes. Each group contains velocity data from 25 shapes. Individual participants are represented in small dots, mean in large dots. All error bars represent 95% CI.

incongruent condition demonstrating an anticipatory response in the direction cued by the shape, which was opposite to the actual motion direction (Figure 1E; $F(2,39) = 56.16$, $p < 0.0001$). Again, the strength of the anticipatory response in both congruent and incongruent conditions scaled with the strength of the directionality of the shapes (Figure 1F; congruency condition: $F(1,104) = 171.36$, $p < 0.0001$; congruency condition × directionality strength: $F(3,104) = 11.27$, $p < 0.0001$). The strength of the anticipatory response for Experiment 1 was stronger than Experiment 2 (Wilcoxon rank sum $W = 53$, $p = 0.039$), indicating an additional element of statistical learning, as the probability of a shape moving in its perceived direction was only 50% in Experiment 2. It is remarkable that the shape's perceived directionality still produced an anticipatory response, even when the likelihood of the shape moving in its perceived direction was only chance, and indicates that this is a robust, automatic response that occurs independent of the current statistical environment[3,9]. Additionally, although some shapes could be perceived as animal-like, the perceived familiarity of the shapes did not influence the strength of the ASEM response (see Supplemental information).

Together these results show that the oculomotor system uses directional inferences derived from shape to anticipate the direction of upcoming movements. In the natural world, the inherent shape of a target can provide crucial cues about an object's likely movement direction. Here we show that the inferences drawn from these cues explicitly and rapidly affect anticipatory oculomotor planning, even in cases when relying on these shape cues was detrimental to behaviour (by requiring a U-turn in the eye movement), and even in cases when participants explicitly knew that movement direction was unpredictable (see Supplemental information). This anticipatory response aids pursuit of the target, providing accurate and up-to-date information about the velocity, location, and properties of the target, which in turn provides the motor system with the visual information crucial for both planning and correcting actions (for example arm and hand movements) to interact with the environment[7,8]. The anticipatory responses in this study echo classic ASEM effects that show a scaling of response by the strength of beliefs about an object's future motion. Here, the response seems to reflect a deeply engrained prior belief about how objects with different shapes move in the world[3] — a belief that is so compelling and salient that the oculomotor system relies on it even to its detriment, and even despite explicit expectations to the contrary (see Supplemental information). Such directional expectations may then drive oculomotor anticipation through attentional cueing[5], or the form of the directional shapes may produce implied motion which activates motor areas in the brain[10].

Being able to anticipate the upcoming motion of objects and organisms is crucial for predicting moment-to-moment changes in the world, which is vital in many situations, including hunting, anticipating the movement of a predator, or avoiding collision with moving objects. These results show that the shape of an object or organism is a crucial cue that drives these anticipatory responses, and provide an insight into the functional benefit of being able to infer direction from shape. This expands our knowledge of directional inference from shape[5] by showing that such inferences trigger an automatic anticipatory response, even when it is disadvantageous. Measuring inference from shape in a paradigm such as this also opens intriguing new possibilities for measuring and understanding the elusive processes that determine how complex causal inferences are derived from shape and quickly and automatically incorporated into prediction-driven behaviour.

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures, detailed methods, supplemental experiments and analyses, and can be found with this article online at https://doi.org/10.1016/j.cub.2023.07.028.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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