the increased recruitment during the period 1963–1983, which resulted in the 'gadoid outburst'. □

## Methods

### Plankton data

Biological data used in this study were collected by the CPR survey. This is an upper-layer plankton monitoring programme that has been operated on a routine monthly basis in the North Atlantic and North Sea since 1946[10]. Sampling is carried out by a high-speed plankton recorder (about $20\,km\,h^{-1}$) that is towed behind merchant ships at monthly intervals on regular routes at a standard depth of approximately 6.5 m. One CPR sample corresponds to about $3\,m^3$ of sea water filtered[10].

### Selection of plankton indicators

In the North Sea, cod spawn in March and eggs start to hatch a few weeks later[2]. From March to September, feeding of cod larvae/juveniles gradually progresses from mainly copepod eggs (April) to copepod and euphausiid nauplii (May), then a copepod-dominated diet until July and finally a progressive replacement of the copepod-based diet by euphausiids and other fish larvae from August[9]. Among copepods, *C. finmarchicus* is by far the dominant species eaten by larval cod, followed by *Pseudocalanus* spp[5]. Therefore, the abundance (number of individuals per CPR sample) of *Calanus finmarchicus*, its congeneric species *C. helgolandicus, Pseudocalanus* spp. and euphausiids was assessed in the North Sea (including the Skaggerak). The size composition of prey is also a crucial parameter[5]. The mean size of calanoid copepod (minimum size of female) per CPR sample was also calculated. We chose the minimum size of female because adult females, or copepodite stage V, represent the majority of copepods caught in the samples[27]. Total calanoid copepod biomass per CPR sample was used as a quantitative indicator of food for larval/juvenile cod and was estimated from the size of each calanoid copepod (a total of 108 calanoid species), their abundance and allometric relationships[28].

### Cod data

Cod data on recruitment (one-year-olds) were derived from virtual population analysis[29]. Data for 1963–2000 are from ref. 14 and for 1958–1962 from ref. 3. These two sources overlap for the 31-yr period 1963–1993. The recruitment values taken from ref. 3 were adjusted using a linear regression analysis for the 31-yr period of overlap to produce a time series of recruitment from 1958.

### Correlation analysis

The Pearson linear correlation was calculated between cod recruitment (one-year-olds) at lag one and the plankton index on original and detrended time series to take into account temporal autocorrelation. Series were detrended by the use of Singular Spectrum Analysis[30]. The method uses a principal component analysis performed on an autocovariance matrix (also called a Toeplitz matrix) to decompose a time series into a succession of signals of decreasing variance. The procedure is fully described in ref.20. The long-term trend of each time series was first assessed by using both the eigenvectors and the principal components representing the low-frequency variability. Then, the detrended time series were calculated by subtracting the original time series by their respective long-term trend.

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# Visual control of action but not perception requires analytical processing of object shape

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**The visual perception of object shape depends on 'holistic'[1–4] processing in which a given dimension cannot be perceptually isolated from the other dimensions of the object. The visual control of action (such as grasping an object), however, which is mediated by cortical areas that are largely independent of those mediating conscious perception[5–8], must take into account only the most action-relevant dimension of an object without being misled by other non-relevant object features. Here we report the results of two experiments showing that vision for perception and vision for action deal with objects in a fundamentally different manner. We tested participants' ability to make perceptual judgements of the width of different rectangular objects or to grasp them across their width, while in both cases ignoring length[9,10]. Participants could not ignore length when making perceptual judgements of width but they could completely ignore length when grasping the same objects. These results suggest that in situations in which the elementary dimensions of an object's**

**shape are perceived in a holistic manner, the same dimensions are treated analytically when a visually guided action is directed at that same object.**

The idea that vision treats object shape in a holistic manner has been a basic theme running through theoretical accounts of perception from early gestalt psychology[11] to more contemporary cognitive science[1,12–14]. Indeed, encoding an object holistically permits a representation of the object that preserves the relations between object parts and its surroundings without requiring precise information about the absolute size of the object's dimensions[15,16]. When we interact with an object, however, it is imperative that the visual processes controlling the action take into account the absolute metrics of the most relevant dimension of the object without being influenced by other dimensions or features[17]. In other words, rather than being holistic, the visual processing mediating action should be analytical.

To test this idea, which on the face of it might seem counter-intuitive, we carried out two experiments in which we compared how visually guided action and visual perception dealt with one of the fundamental attributes of an object, its shape[18–21]. In both experiments we used a modified version of a well-established psychophysical tool, Garner's speeded-classification task[9,10,22,23], which provides a reliable measure of how efficiently people can process one dimension of an object while ignoring its other dimensions[24]. In a typical Garner experiment participants are asked to classify objects on the basis of a single dimension under two different conditions. In one condition (baseline), the relevant dimension varies but another, irrelevant, dimension is kept constant. In the other condition (filtering), the relevant dimension again varies but this time so does the irrelevant dimension. If participants are able to process the two dimensions independently (that is analytically), then the speed and accuracy should be identical for the baseline and filtering conditions. If participants cannot process the two dimensions independently and must treat them holistically, then performance should be worse for the filtering condition than for the baseline condition, because participants cannot 'filter out' the changes in the irrelevant dimension.

The dimensions that we used were the width and length of rectangular objects. We chose these dimensions for three reasons. First, they represent an elementary instance of dimensions that constitute the shape of objects[18]. Second, these dimensions have been shown to be represented holistically in a number of perceptual studies[25–27]. Finally, the width and length of objects can be manipulated in a modified Garner's task to compare directly the processing underlying perception and visually guided action within the same experiment.

Four different rectangular objects were used in both of our experiments. They were created from factorial combination of two different widths with two different lengths. The two longer objects were presented in random order in one block of the baseline condition and the two shorter ones in a second block of the baseline condition. All four objects were presented in the filtering condition. In all cases, width was the only relevant dimension.

In experiment one we used Garner's paradigm to compare object perception and object-directed action. In the perceptual classification task 12 participants made speeded judgements (wide or narrow) of the width of each rectangular object by pressing one of two response buttons (Fig. 1). In the grasping task, the objects were presented in the same way but now the participants were instructed to reach out and grasp each object as quickly as possible across its width using their finger and thumb in a natural precision grip. Hand and finger movements were tracked using opto-electronic recording of the position of infrared light-emitting diodes attached to index finger, thumb and wrist.

Mean reaction times for each participant were calculated for correct responses on perceptual trials and successful final pick-ups on grasping trials during baseline and filtering conditions. Outliers of more than two standard deviations above the mean were eliminated. Accuracy for both perceptual classification and grasping was high (less than 1% error) and did not vary between conditions.

As can be seen in Fig. 2, the reaction times for perceptual classification in the filtering condition ($436 \pm 20.4$ ms; mean $\pm$ standard error) were 23 ms slower than reaction times in the baseline condition ($413 \pm 25$ ms). This significantly worse performance in the filtering compared with the baseline condition ($t_{11} = 2.49$, $P < 0.05$), sometimes called Garner interference, indicates that the width of the objects could not be processed independently of length when perception was required. In contrast, however, reaction times to complete the movement in the grasping task in the filtering condition ($856 \pm 21.5$ ms) were similar to those in the baseline condition ($859 \pm 22.3$ ms). The $-3$ ms difference between the conditions was not significant ($t_{11} = 0.3$, $P > 0.1$). The same absence of a difference between filtering and baseline conditions was evident when only the time to initiate the grasping movement was considered or the time to reach maximum grip aperture. An analysis of variance (ANOVA) between tasks (reaction times for perceptual judgements versus reaction times to grasp objects) and conditions (baseline versus filtering) revealed a two-way interaction between these factors, confirming that width and length of rectangles are treated differently for perception and visually guided action ($F_{1,11} = 7.93$, mean square error = 251, $P < 0.05$).

To test whether grip scaling was sensitive to width and to test for possible differences in grip scaling between baseline and filtering conditions, we calculated the maximum grip aperture for wide and narrow objects in each experimental condition. The maximum



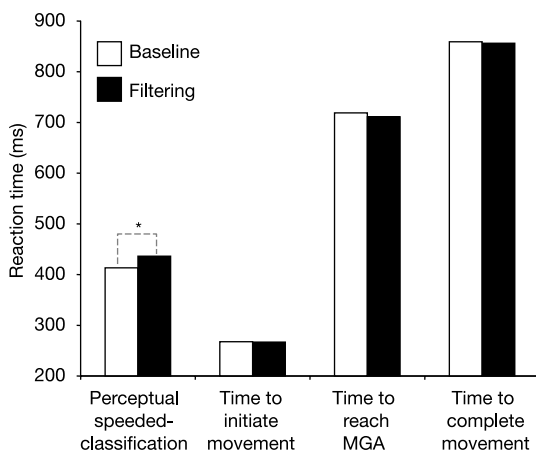Grasping             Perceptual speeded-classification           Simulated grasping
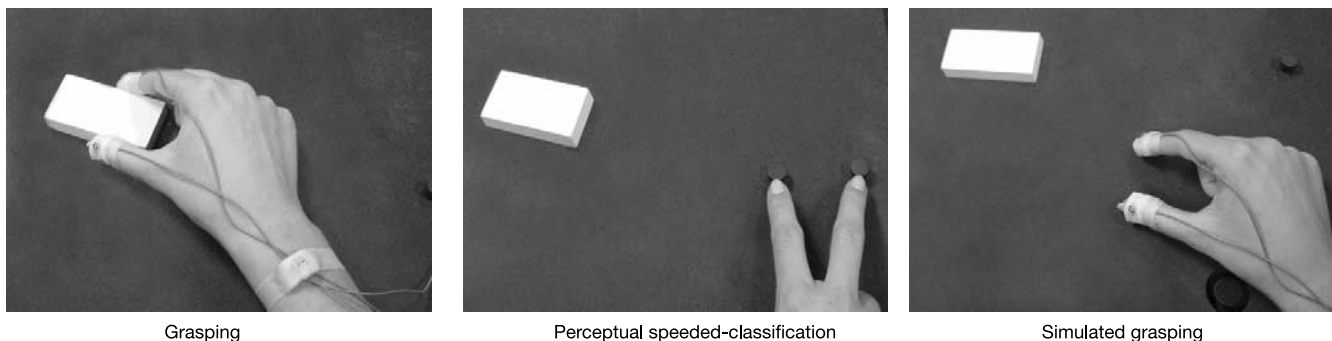
**Figure 1** Tasks used in experiments one and two. From left to right, the tasks shown are: the grasping task (left) and the perceptual speeded-classification task (centre) (experiment one), and the simulated grasping task (right) for perceptual estimation (experiment two).

opening between the thumb and index finger during grasping, which is typically achieved 70% of the way through the movement trajectory, is known to be well correlated with the size of the goal object. Maximum grip aperture was 80.8 mm in the baseline condition and 80.2 mm in the filtering condition for wide objects, and 76 mm in the baseline condition and 75.6 mm in the filtering condition for narrow objects. An ANOVA between width and condition revealed a significant main effect of width ($F_{1,10} = 119$, mean square error $= 2.06$, $P < 0.001$), which indicated that grip scaling was highly sensitive to the width of an object. The main effect of condition ($F_{1,10} = 0.2$, $P > 0.1$) and the interaction between width and condition ($F_{1,10} = 0.1$, $P > 0.1$) were not significant.
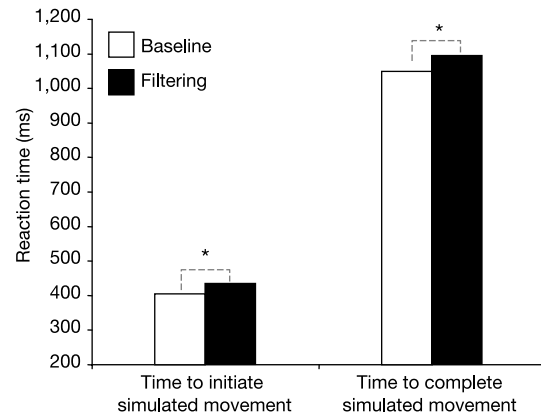
The results of experiment one show that participants could successfully grasp rectangular objects across their width without being affected by irrelevant variations in length but they could not (or at least did not) make perceptual judgements of width without being affected by irrelevant variations in length. Therefore, these results show that the two elementary visual dimensions that constitute the shape of rectangles can be treated in a completely independent manner for visually guided action but not for visual perception.

An alternative explanation for the pattern of results in experiment one is that the different task demands, rather than different kinds of visual processing, led to the dissociation found between perception and visually guided action. Specifically, one has to refer to memory for what is considered wide or narrow in the experiment when making perceptual judgements, but not when grasping. A second experiment was therefore carried out to rule out this possibility. In experiment two a simulated grasping task was used to assess perceptual judgements. In this task, participants estimated the width of each object by reaching out and placing their finger and thumb a particular distance apart at a remote location without actually grasping the object (Fig. 1). This task does not require memory-based comparison and is known to make use of perceptual information[28]. We expected, therefore, that we would find Garner interference in this task.

Eight participants took part in experiment two in a similar



**Figure 3** Effects of irrelevant variations in length on the reaction time for simulated grasping. The mean time to initiate the movement was slower in the filtering condition (filled bars) than in the baseline condition (open bars) ($t_7 = 2.39$, $P < 0.05$). The same was true for overall movement time ($t_7 = 2.40$, $P < 0.05$).

paradigm to that used in experiment one, but were asked to make simulated rather than actual grasping movements. As can be seen in Fig. 3, significant Garner interference effects were found in this experiment for both the time to initiate and the time to complete the movements. These results confirmed our prediction that width and length are perceived holistically even when memory-based comparisons are not required. Notably, our design also allowed us to examine the effects of length on computations of width using another measure. Specifically, if width cannot be perceived independently of length, then one would expect an illusion to occur, in which longer objects are perceived to be narrower than shorter objects with the same width. This was exactly what we found for the width estimates in experiment two (Fig. 4). This was not the case, however, for maximum grip aperture in the grasping task of experiment one; in this case, there was no effect of the object's length on computation of width. Taken together, the findings of
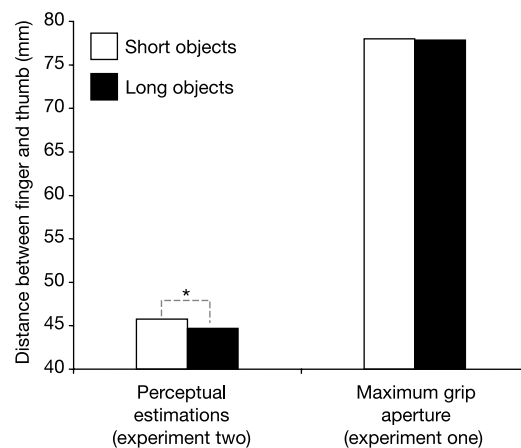


**Figure 2** Effects of irrelevant variations in length on the perception of object width and on object-directed grasping (across the object's width). Reaction times for speeded-classification (first column) of width were significantly slower in filtering (filled bars) than in baseline (open bars) conditions. Reaction times for grasping (second to fourth columns) were not different between filtering and baseline conditions. Other kinematic measures of grasping also showed no difference between conditions. A control experiment that rules out the possibility that visual feedback during the execution of the grasping movement may have eliminated the Garner interference effect in this condition is described in Supplementary Information. MGA, maximum grip aperture.



**Figure 4** Effects of length on grip scaling for width in simulated grasping and real grasping in the filtering condition. In experiment two, in which perceptual estimates were required for the simulated response, longer objects (filled bars) resulted in significantly smaller finger–thumb apertures than shorter objects (open bars) ($t_7 = 3.01$, $P < 0.05$). In experiment one there was no difference in maximum grip aperture for longer and shorter objects ($t_7 = 0.65$, $P > 0.1$). A significant interaction between length (longer objects, shorter objects, within-subject variable) and task (simulated grasping, real grasping, between-subjects variable) showed that the difference between these effects was significant ($F_{1,17} = 4.86$, mean square error $= 0.39$, $P < 0.05$).

experiments one and two provide compelling support for the idea that perception of an object's width is affected by its length but grasping across the object's width is not.

The fact that the time taken to initiate and complete a grasping movement is not affected by variations in the irrelevant dimension supports the notion that the visual information used to program the grasp is not derived from the visual processing mediating perception. Right from the start, in other words, grasping selectively processes information about the relevant dimension without first processing the entire shape of the object.

The idea that visual perception uses holistic processing of object features whereas the visual control of action is more analytical helps to explain why separate cortical pathways have evolved for these two different kinds of visual processing: a ventral stream for perception and a dorsal stream for action[5–8]. It also helps to explain why visual illusions (which, by definition, have strong effects on perceptual judgements) often have little or no effect on the scaling of grasping movements[29].

Most contemporary theories of visual perception (see ref. 20 for a review) agree that, for proper recognition of objects to occur, the raw visual input must be transformed into visual representations that preserve the relative aspects of an object's dimensions, as well as their relation to the dimensions, orientation and location of other objects in the scene. An obvious cost of relying on such allocentric[17] and holistic representations is that important attributes of our visual environment, such as the absolute metrics of objects, are less accessible. Our findings suggest that the absolute metrics of action-relevant dimensions may be separately computed by the system mediating our interactions with objects in our near environment. Our findings also suggest that this is accomplished because, unlike with visual perception, the visual mechanisms mediating action are able to process the most relevant dimension while at the same time ignoring changes in the other, irrelevant, dimensions. In short, vision for action operates in an analytical rather than a holistic fashion. □

## Methods

### Experimental design

Participants were seated in front of a black tabletop on which the objects were placed at a viewing distance of approximately 40 cm. Computer-controlled PLATO goggles (Translucent Technologies) with liquid-crystal shutter lenses were used to control stimulus exposure time. Grip scaling and reaction times were recorded by an Optotrak (Northern Digital), which tracked the three-dimensional position of three infrared light-emitting diodes attached separately to the participant's index finger, thumb and wrist with small pieces of surgical tape, which allowed complete freedom of movement of the hand and fingers. Participants were right-handed undergraduate students and received a course credit for their participation. Each participant gave informed consent and the experiments were approved by the local ethics committee. To prevent participants from adopting an automated grasping strategy, the target objects were presented in random locations on the tabletop (within a circle of 5 cm) at randomly interleaved orientations between 15–25° from a plane parallel with the participant's midline (Fig. 1).

### Object design and presentation

The objects were created from a factorial combination of two different widths (that is, 35.7 and 30 mm) by two different lengths (that is, 75 and 63 mm). The proportions used were the same as those used in the original perceptual study that applied Garner's task to examine the relationship between width and length[25]. The thickness of all stimuli was 15 mm. Each object was presented 16 times (2,000 ms for each object) in the baseline condition and 16 times in the filtering condition. To equate the overall number of objects in the baseline and filtering conditions, the filtering condition was divided into two equal smaller filtering blocks (32 stimuli presentations in each block). Before the beginning of each block participants were shown the objects that would be presented in that specific block. The interstimulus interval was 3,000 ms. Four practice trials were administered before the beginning of each block and there were 1-min rests between blocks.

### Experiment one

For the perceptual speeded-classification task in experiment one, participants were asked to place the first and second fingers of their right hand on the response box, and immediately after the opening of the goggles, to press the right key if the object was wide, or the left key if the object was narrow (Fig. 1). To ensure that they received the same tactile feedback in the perception task as they did in the grasping task, participants were asked to reach out and grasp each object by its width immediately after making each speeded-classification response. In the grasping task of experiment one, participants placed the

index finger and thumb of their right hand on a start button, and were asked to reach out and grasp each object across its width as quickly as possible immediately after the goggles were opened. Order of the conditions (baseline/filtering) and task presentation (speeded classifications/grasping) was counterbalanced across participants. Grip scaling data of one participant in experiment one was excluded from the analysis due to the loss of more than 50% of data point signals.

### Experiment two

For the simulated grasping in experiment two the same apparatus was used, but now participants were asked to simulate the grasping movement that they would make if they were to pick up each object across its width. Instead of grasping the object, however, they indicated how they would do so by reaching out and placing their index finger and thumb beside the object as though they were picking it up. To ensure that they received the same tactile feedback in simulated grasping as in real grasping, participants were asked to reach out and grasp each object immediately after completing the simulated grasping movement.

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