Abstract of “Objects in Space” by Heida Maria Sigurdardottir, Brown University, July 2013

In this thesis, we explore how objects affect the space around them. We show that spatial information is extracted from even completely novel objects. Information derived from the shape of objects is swiftly and automatically integrated into a variety of processes, such as the allocation of visual attention, the programming of eye movements, and the perception of motion. We provide evidence supporting that the lateral intraparietal area (LIP) of the macaque is able to extract such spatial information from objects. We also show that IPS1, the putative human homologue of LIP, can represent space not just in pure retinotopic coordinates but can code for space relative to the location of an object.

Objects in Space

by

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Providence, Rhode Island

July, 2013

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Preface

Minn er betri. – Heiða María Sigurðardóttir

Acknowledgements

Many people deserve to be thanked, and I will surely forget someone (sorry, someone!). I would, first of all, like to thank my advisor, David Sheinberg. David is always enthusiastic and ready to help. I am amazed how he answers every single email 10 minutes after I send it, even at three in the morning (on an unrelated note, his coffee intake has become legendary). Not only has David been there for me professionally, he has also gone through great lengths to be supportive in other ways such as by giving me his sons' baby clothes or helping me find and pick up a bed for my mom on Craigslist. Those kind little gestures are the ones that I am the most thankful for and the ones I will always remember.

I would like to thank my committee members, David Badre, Joo-Hyun Song, and Michael Tarr, for all their help and support (and Mike, thanks for always having my back). Thanks go to John Ghenne, who has given me so much help with taking care of the monkeys and running experiments – I could not have done it without him. Thank you, Suzanne Michalak, for all your help with behavioral experiments and for being a good friend – we had fun. I would like to thank Luc Amdahl for helping me with running subjects and drawing regions of interest, and thanks go to Erin Hoops for doing a good chunk of the programming for the fMRI mapping stimulus. I would like to thank all past and present Sheinberg Lab members, the people of PEN, all the graduate students, and my fellow moms. Special thanks go to Brandon King – you are an amazing person and I know you will always be there for me.

Takk elsku mamma og pabbi fyrir að styðja mig alltaf í einu og öllu. Pabbi, þú hefur alltaf verið hetjan mín. Mamma, þú ert yndislegust og best. Maggi og Lilja, takk fyrir að vera ekki of vond við litlu systur. Mikið verður gaman að hitta ykkur aftur. Takk Elísa Auður fyrir að koma og passa og fyrir að standa þig svona ótrúlega vel. Ég er svo stolt af þér. Björn Leví og Alexander Arnar: Ég elska ykkur meira en orð fá lýst. Þetta er ekki væmið af því að ég meina það. Okkur tókst þetta saman!

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CHAPTER ONE

Introduction

The enormous significance of the constantly growing stock of earlier experiences in the life of humans and of higher animals can hardly be overlooked. Perception itself is also improved through use, practice, and schooling and makes possible an increasingly finer, richer, and deeper grasp of things. But these facts should not be permitted to blind us to the idea that the fundamental laws of perception are present before the accumulation of this stock of experience, and before such schooling. Those fundamental laws are not profoundly changed by experience, but rather, without the existence and stability of these laws, the store of past experience could neither be collected nor utilized.

Wolfgang Metzger – The Laws of Seeing

When the wise man points at the Moon, the idiot looks at the finger.

Confucius

Objects in Space

On March 1972, the Pioneer 10 spacecraft was launched. Attached to it was a gold-anodized aluminum plaque containing a message to any extraterrestrial intelligent life forms that might encounter it (figure 1.1). The plaque, amongst other things, showed a diagram of the Earth's relative position to the Sun and planets, as well as its location relative to several prominent pulsars, many of which can be seen from other parts of the galaxy. Also depicted was Pioneer's trajectory as it passed Mars and Jupiter and finally exited our solar system to continue its journey to outer space.

This message to the stars might be more telling about the human inhabitants of the planet Earth than its makers foresaw. Had we been intelligent dog-like creatures, we would most surely have equipped Pioneer with chemicals of various smells. The human race instead sent the message in pictorial form. This speaks to the tremendous importance of vision for primates whose brains have evolved to contain dozens of cortical regions devoted to the processing of visual information (Van Essen et al., 2001).

The Pioneer plaque has been criticized on the grounds that in order to decrypt the message, one needs to have experienced human culture (Gombrich, 1972; Vakoch, 1998). Gombrich (1972) notes that Pioneer's trajectory is marked with a directional arrowhead, a symbol impossible for an alien race to decipher since they have presumably never in their history had anything equivalent to a bow and an arrow.

One might also realize that an event extended in time is depicted as a static image; Pioneer's past locations are represented by the arrow's shaft, with the more distant past corresponding to locations closer to the shaft's end, while the object's future locations are implied by the direction to which the arrowhead points. There is no guarantee that a spatial representation of time would make any sense to an extraterrestrial.

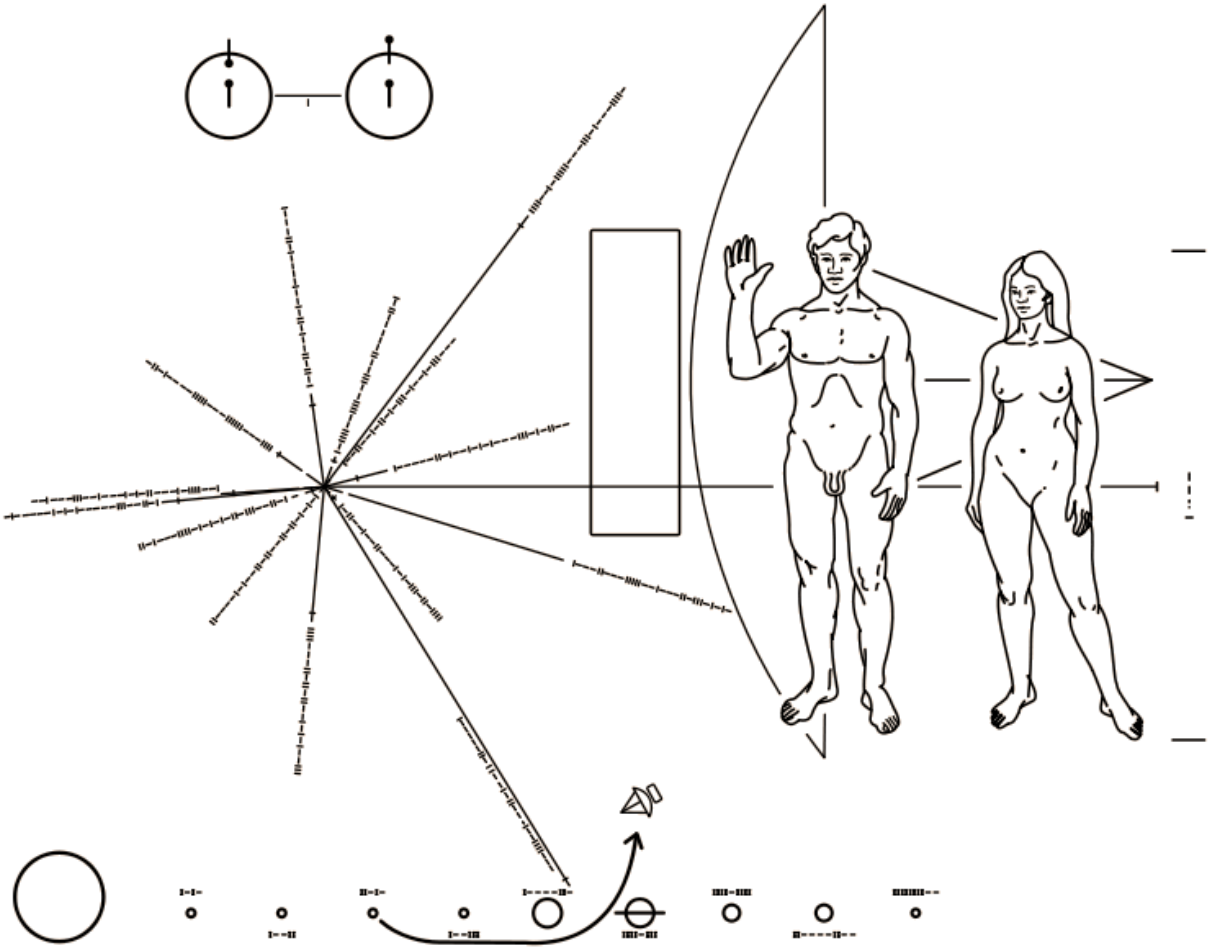

Figure 1.1. The Pioneer plaque. The image was created by NASA and is in the public domain.

Finally, the Earth's position is shown relative to several other objects in space, but reading such a celestial map requires the ability to perform complex coordinate transformations of visual information. If an alien found the Pioneer plaque and wanted to get to Earth, it would need to not only have some way of representing space as relative to objects in the world, but it would have to understand how the map should be scaled up, translated and rotated so as to match the real world objects depicted on this flat 2D surface. This is no mean feat.

This thesis concerns objects in space – not the celestial bodies depicted on the Pioneer plaque, but how objects affect the space around them and the neural machinery used for this purpose. It will, in a sense, explore how the message sent to other worlds might make intuitive sense to us humans because of the way our visual systems have been set up to work.

Visuospatial Codes

Let us imagine a simple sighted organism. Its visual needs are quite straightforward. If it sees something good, such as food or a potential mate, it needs to orient toward it and approach it. If it sees something bad, such as an obstacle or a predator, it should move away and avoid it. Its limited behavioral repertoire might be adequately supported by relatively elementary neural machinery that codes for where things are in space in relation to the organism.

For humans and non-human primates alike, light gets transduced to neural signals in the retina of the eye. Retinal ganglion cells with partially overlapping dendritic trees tile the retina and their dendritic coverage determines their receptive field, or the region of the retina on which light must shine in order to change their rate of firing (for a review on the evolution of the vertebrate eye, see Lamb, Collin, & Pugh, 2007; for a review on the functional architecture of the mammalian retina, see Wässle & Boycott, 1991). In primates, all visual information therefore starts out as retinotopic, where nearby neurons tend to respond to light falling on locations close to each other on the retina. Several brain regions apparently inherit this type of spatial representations where nearby patches of cortex selectively respond to light that falls on nearby patches of the retina (Gardner, Merriam, Movshon, & Heeger, 2008; Golomb & Kanwisher, 2012; Wandell & Winawer, 2011). Just like for our simple sighted organism, this is a way of representing where things are relative to our own body – in this case, where things are relative to the center of our eye.

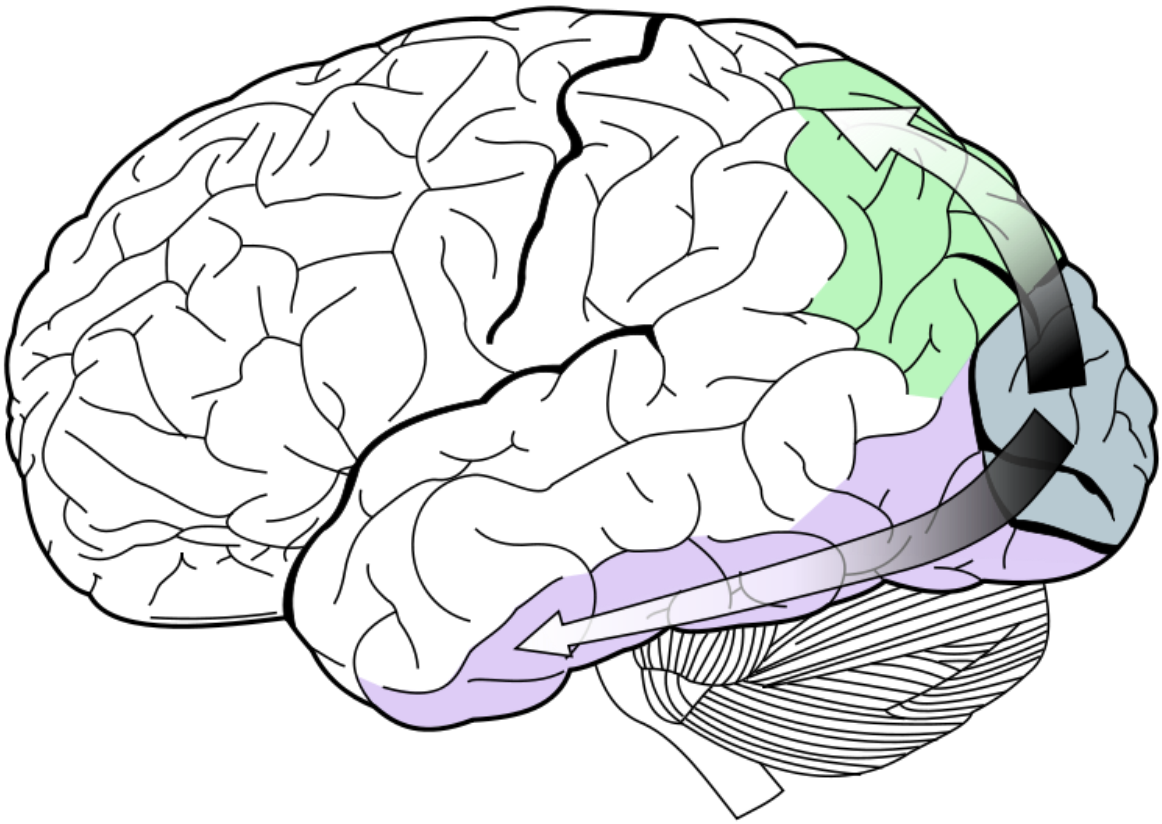

Figure 1.2. Two visual streams. A very influential idea in cognitive neuroscience is that there are at least two cortical visual processing streams (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). Each gets input from the primary visual cortex (among other areas), but one moves ventrally to the temporal cortex, while the other is more dorsal and ends in the parietal cortex. The ventral stream seems to be important for object identification and has been dubbed the 'what' stream. The dorsal stream was originally thought to be dedicated to spatial information and has therefore been called the 'where' stream, but has more recently been called the 'how' stream because of its importance in action guidance. The human primary visual cortex (V1) is shown in gray, the ventral 'what' stream can be seen in purple, and the dorsal 'where/how' stream is marked in green. The image is published under a Creative Commons Attribution-Share Alike license, and is originally from**:** http://commons.wikimedia.org/wiki/Image:Ventral-dorsal_streams.svg

Our hypothetical organism might be well served with a one-size-fits-all mechanism for the coding of spatial locations. Initially it was also thought that such all-purpose spatial representations resided in the posterior parietal lobe (further subdivided into the superior and inferior parietal lobules; Rizzolatti, Fogassi, & Gallese, 1997; see also figure 1.2). Spatial distortions from parietal damage have long been known. Holmes (1919), almost a hundred years

ago, described the symptoms of patients who suffered from gunshot wounds to the posterior and upper parts of the parietal lobe. These patients seemed unable to construct spatial representations from visual information; their eyes would randomly drift instead of purposefully scanning the scene, they would reach for an object in the completely wrong direction, and would even directly walk into walls as if they had no idea of their position in space.

However, humans, macaques, and many other primates, unlike our simple organism, are capable of complex interactions with their environments. Complex action capabilities might require not just a single representation of space, but many specialized ways of coding where things are in the world. A monkey swinging from branch to branch presumably needs to have a visual system capable of calculating the direction and distance of the next branch not just relative to the center of gaze, but relative to her body and the hand with which she grasps it. Since the visual information is originally only available in a retinotopic frame of reference, this new representation requires the transformation of the original retinotopic space into egocentric coordinate frames centered on other parts of the body.

The main function of the parietal cortex in primates is now thought to be to carry out such transformations from sensory signals to a format more directly useful for motor output or action guidance (Milner & Goodale, 1995; Orban et al., 2006; Rizzolatti et al., 1997). These kinds of visuomotor transformations can occur without awareness and are thought to be highly automatic (Milner & Goodale, 1995). Such spatial representations are generally thought to be egocentric, which is to say that spatial locations are coded with reference to a part of one's own body, such as the eyes, head, hand, trunk, or mouth (Goodale & Milner, 1992).

Egocentric coding is not the only way to represent space, and neither is it necessarily always the best way. For example, macaque mothers monitor their infants, especially when they are beyond reach, in order to detect and avoid any possible threats to the infants (Onishi & Nakamichi, 2011). The mothers seemingly have the ability to monitor not just where the infants are relative to the mothers themselves, but relative to external objects. In order to be able to intervene in time, it is also important for the mothers to predict whether the infant will come to any harm before it actually happens; a stalking leopard, even though quite still, is a very serious threat.

Humans rarely are threatened by predators but the ability to use visual information to predict where important things will be in the near future nonetheless has obvious survival value.

Swiftly and accurately predicting where a moving car is going can make the difference between life and death, even for us. Sometimes, though, one might simply wish to monitor a situation without it having an immediate effect on oneself. It might be of importance for you to know where the car is most likely going even after establishing that it is not heading directly toward you.

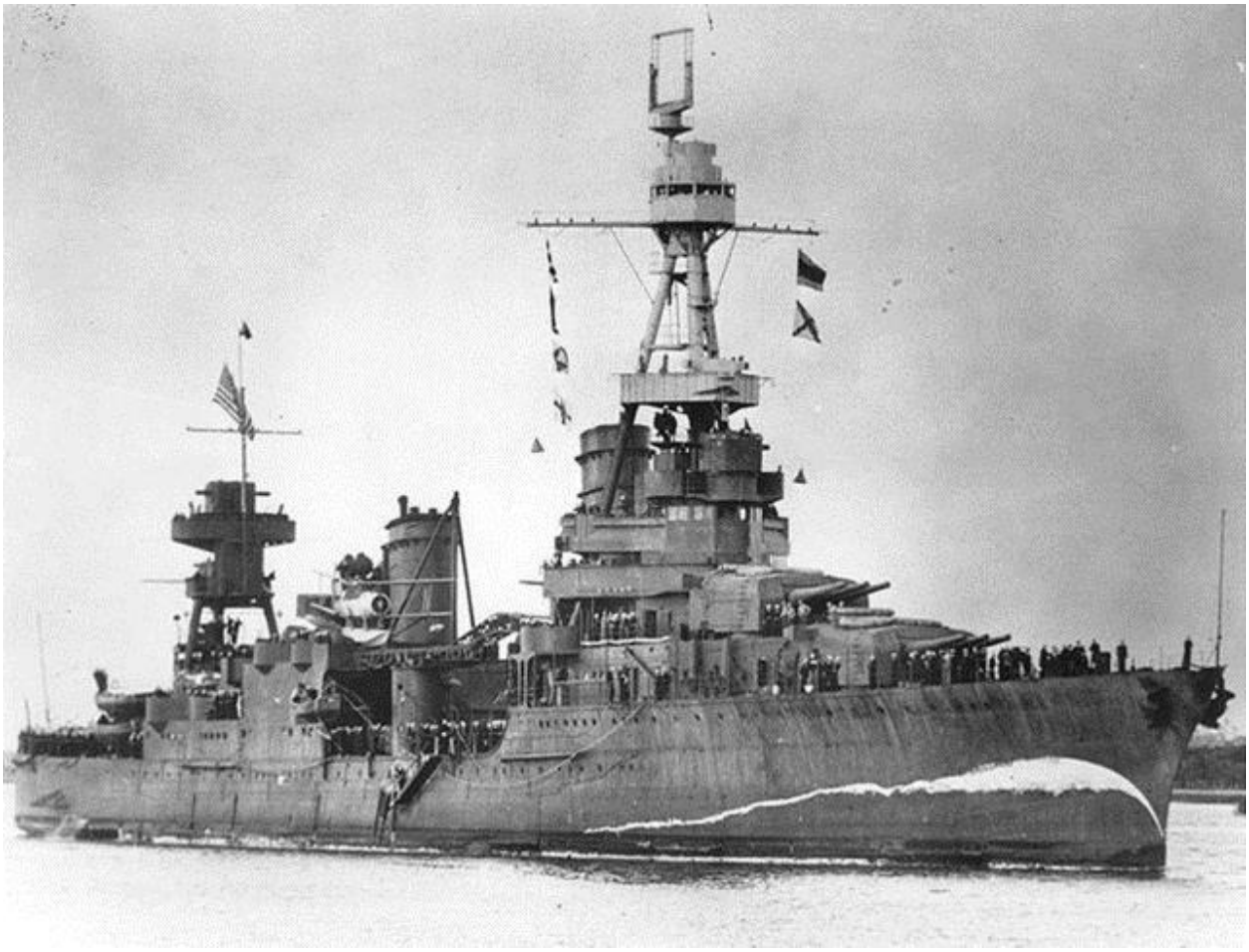

Figure 1.3. USS Northampton. This naval warship was painted with a white bow wave so as to give the false impression of high-speed movement in a particular direction even though the ship might in reality be completely still (Sumrall, 1971). The image is in the public domain.

Humans seem capable of making such predictions based on visual information on objects. Sometimes we cannot help it – it apparently happens whether we like it or not. This has been made use of in many venues. An artist might use visual cues to direct your eyes and attention to a particular location in a painting that he wishes to emphasize. The same might be

done by a keen web designer or a clever advertising company. A magician will misdirect his audience's attention to create his illusion. Such tricks have been used in war. The shape of a false bow wave was painted on naval warships so as to trick enemies into misestimating the ships' direction and speed of movement, thus making them harder to target (Sumrall, 1971; see figure 1.3). Visual objects that redirect attention also keep wandering pedestrians from getting run over by cars, as can be seen in figure 1.4.

Figure 1.4. Directing attention. This street sign notifies people that they should check for approaching cars. Here, an arrow and the words "look left" guide people's eyes and attention in a particular direction away from the objects themselves. The image is published under a Creative Commons Attribution-Share Alike license, and is originally from**:** http://www.flickr.com/photos/_pek_/3839589571/sizes/o/in/photostream/

The street sign in figure 1.4 also exemplifies that sometimes objects can give us important clues about where other things or events will be in the near future. This, at least at a first glance, seems to be an indirect and symbolic way of representing space. Orienting to a spot of light is elementary and direct – even plants, which have no nervous system, will do that. Sampling information from the spot of light and deciding, on that information, to look

somewhere else, instead, is intelligent behavior. When a wise man points to the Moon, only an idiot will look at the finger.

Artists, designers, advertisers, magicians, warmongers, and traffic regulators all have discovered that the visual properties of objects can effectively be used to redirect and misdirect attention away from the objects themselves. In this thesis, I will look at how objects affect the space around them, how they guide the eyes and attention in particular directions relative to themselves, under what circumstances they do so, what brain areas are responsible for extracting such information, and the format of the spatial code that these brain regions use.

In chapter 2, "Action-related object coding in the lateral intraparietal area", I will describe my research on how the shape of an object can automatically form a hypothesis regarding where to look and pay attention, and how shape selective regions in posterior parietal regions of the dorsal visual stream can represent such hypotheses. The lateral intraparietal area (LIP) is selective for the shape of objects and plays a role in both overt and covert orienting. This makes it a primary candidate region for carrying out the necessary computations for extracting an orienting bias from shape.

In chapter 3, "Form-derived directionality of objects: Its effects on visual attention and motion perception", I look in more detail at how the shape of objects induces a systematic orienting bias that is consistent across people and has a measurable strength and directionality. Shape attributes rapidly and automatically bias both overt and covert orienting, pushing people toward certain locations and away from others. These predispositions do not appear to require the recognition of the shape in question, and affect learning of new associations between what we see and where we look. Not all associations are made equal; on the contrary, going against our inherent biases takes time and effort and might never be fully accomplished. Such biases also affect the perception of movement, where the shape-defined directionality of an object is integrated into calculations about its probable path of motion.

The experiments described in chapter 2 and 3 were based on the hypothesis that objects can affect the weights given to locations in a spatial priority map (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Itti & Koch, 2001). It was initially assumed that this spatial priority map was represented in retinotopic or eye-centered coordinates. However, there were some hints that this might not the case, but that the effects could either instead or in addition manifest themselves in a stimulus-centered coordinate system where space is coded not relative to the

current eye position but relative to an object. In chapter 4, “A tale of two coordinate systems”, I will look more closely into how spatial position is coded in both eye-centered and object-centered frames of reference and the neural representations of both types of coding systems. Several dorsal stream regions, including a likely homologue of LIP in the human intraparietal sulcus (IPS1), simultaneously code for the locations of objects in both egocentric and allocentric reference frames.

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CHAPTER TWO

Action-related object coding in the lateral intraparietal area

Introduction

Many regions within the ventral stream respond selectively to differently shaped objects and are thought to support their successful recognition and categorization (Goodale & Milner, 1992; Logothetis & Sheinberg, 1996; Milner & Goodale, 1995; Palmeri & Gauthier, 2004; Ungerleider & Mishkin, 1982). It therefore came as a surprise when a subregion of the dorsal stream, the lateral intraparietal area (LIP), was also found to be shape selective (Durand et al., 2007; Janssen, Srivastava, Ombelet, & Orban, 2008; Konen & Kastner, 2008; Lehky & Sereno, 2007; A. B. Sereno & Amador, 2006; A. B. Sereno & Maunsell, 1998; M. E. Sereno, Trinath, Augath, & Logothetis, 2002). Although its function is still a subject of debate (Andersen & Buneo, 2002; Bisley & Goldberg, 2003, 2010; Colby & Goldberg, 1999; Gottlieb, Kusunoki, & Goldberg, 1998; Snyder, Batista, & Andersen, 1997), LIP has mainly been implicated in the visual guidance of spatial attention and saccadic eye movements, collectively known as visual orienting (Posner, 1980). LIP shape selective activity did not seem to fit well with this role or the dorsal stream's role in action guidance in general, and the nature of these responses was not obvious.

We suggest that the activity of LIP may best be understood as competing orienting biases or affordances (Cisek, 2007; Cisek & Kalaska, 2010; Gibson, 1979), or the relative merit of the possible sources of information worth exploring with the eyes and attention. We propose that the shape of objects, because of intrinsic properties and previous experience, systematically biases orienting. We hypothesize that LIP plays a crucial role in extracting such a shape-induced orienting bias and that this bias is a major source of LIP shape selectivity. We argue that LIP incorporates a unique shape code that is tightly coupled to behavior.

Shape is indeed taken into account when deciding where to look and pay attention. Saccades to visual shapes are about as fast and consistent as those to simple point targets (He & Kowler, 1991). Such oculomotor guidance does not merely depend on low-level averaging of visual elements but appears to have access to a genuine shape representation (Melcher & Kowler, 1999). After having looked at an object, people also tend to orient to another point within that same object rather than to an equidistant location outside its boundaries or shape (Egly, Driver, & Rafal, 1994; Theeuwes, Mathôt, & Kingstone, 2010). In some cases, a shape can even guide orienting away from itself. An arrow is a prime example, and unlike what was

previously thought, it can reflexively bias orienting (Ristic & Kingstone, 2006; Tipples, 2002). While the shape of things can clearly bias orienting behavior, the shape code used for visual orienting might not be the same as the one supporting perception; some shape cues appear inaccessible to the oculomotor system (Vishwanath, Kowler, & Feldman, 2000).

Several properties of LIP make it a primary candidate region for carrying out the computations necessary for extracting an orienting bias from shape. LIP ranks among the brain areas with the greatest capabilities of integrating and distributing information (Modha & Singh, 2010). It is structurally connected to various visual areas (Felleman & Van Essen, 1991; Lewis & Van Essen, 2000), some of which are shape selective (Desimone & Schein, 1987; Pasupathy & Connor, 2002), and to oculomotor structures such as superior colliculus (Ferraina, Pare, & Wurtz, 2002; Field, Johnston, Gati, Menon, & Everling, 2008), frontal eye fields (Ferraina et al., 2002; Lewis & Van Essen, 2000; Stanton, Bruce, & Goldberg, 1995), and oculomotor domains of the cerebellum (Prevosto, Graf, & Ugolini, 2010). It is thus perfectly situated to gather and combine various sources of visual information with the objective of guiding overt and covert orienting.

Materials and Methods

Overview

We recorded single cell activity in LIP of awake behaving monkeys, both when passively viewing and when acting on particular shapes, to see if and how shape-related LIP responses were linked to past and future orienting behavior (see figure 2.1). We probed the location selectivity of each LIP neuron, finding a preferred (PREF) and an anti-preferred (ANTI) peripheral location. We then briefly mapped the passive neural responses to shapes shown in the PREF location, the ANTI location, and the center of the visual field (CENTER). These shapes later served as 100% valid central precues in a subsequent task, cueing the monkey to saccade either toward the PREF or ANTI location. Some of the shapes used during each recording session were completely novel so the monkey saw them for the first time in the passive shape-mapping task when none of them had yet acquired any particular associations. Others were familiar, meaning that they had previously served as central precues in the active shape-saccade association task and the monkeys had been trained, over the course of months, to saccade to a

particular location when seeing them.

Surgery, MRI, and Recordings

Two male macaca mulatta monkeys (monkey J: 10.5 kg, monkey R: 9.5 kg) were implanted with titanium head posts for restraining head movements during the training and recording sessions. The monkeys had two separate surgeries under isoflurane anesthesia. During the first surgery we implanted a recording chamber of diameter 16 mm at approximately 5P and 12L over the right hemisphere. The chamber was made of MRI compatible plastic material (PEEK, polyetheretherketone). The craniotomy was performed during a second surgery after structural MRI had verified that the chambers were located above the lateral intraparietal area (LIP).

The structural MRI was also used to properly position a metal guide tube so that an electrode would reach LIP. During each recording session, a tungsten microelectrode (1.5 MΩ, Alpha Omega) was lowered using a hydraulic microdrive (David Kopf Instruments), and the neural signals were filtered and amplified (BAK Electronics). Eye movements were monitored and recorded using EyeLinkII (SR Research) with a 500 Hz sampling rate and streamed to a disk at 200 Hz. Experimental protocols were in accordance with animal care guidelines of the National Institutes of Health (Council, 2011) and Brown University's Institutional Animal Care and Use Committee.

Tasks and Stimuli

All stimuli were shown on a 1024 x 768 resolution screen with a refresh rate of 100 Hz, and the experiments were controlled using in-house software running on Windows XP (Microsoft) and QNX RTOS (QNX Software Systems).

The monkeys were trained on three tasks, run consecutively in each session. In the location selectivity mapping task, a yellow fixation square (side length 0.3°) appeared in the center of a light gray background. After the monkey acquired fixation, a dark gray target disk (radius 1°) was flashed for 110 ms at 7° eccentricity. In each trial the disks were randomly chosen to appear in one of eight possible radial directions from the center (22.5°, 67.5°, 112.5°, 157.5°, 202.5°, 247.5°, 292.5°, or 337.5°; 0° corresponds to a location at the right of fixation; numbers increase in counterclock direction). After a brief delay of 60 ms, the fixation square

jumped to that same peripheral location, and the monkey was given juice for saccading to it. We recorded from LIP neurons which, based on online spike data, were deemed to respond to one or more locations. The preferred (PREF) location was defined as the location which evoked the highest mean responses over a 250 ms window (from 40 ms to 290 ms after visual onset of the peripheral disk). The anti-preferred (ANTI) location was a location of the same eccentricity but in the opposite radial direction, in other words 180 degrees away from the PREF.

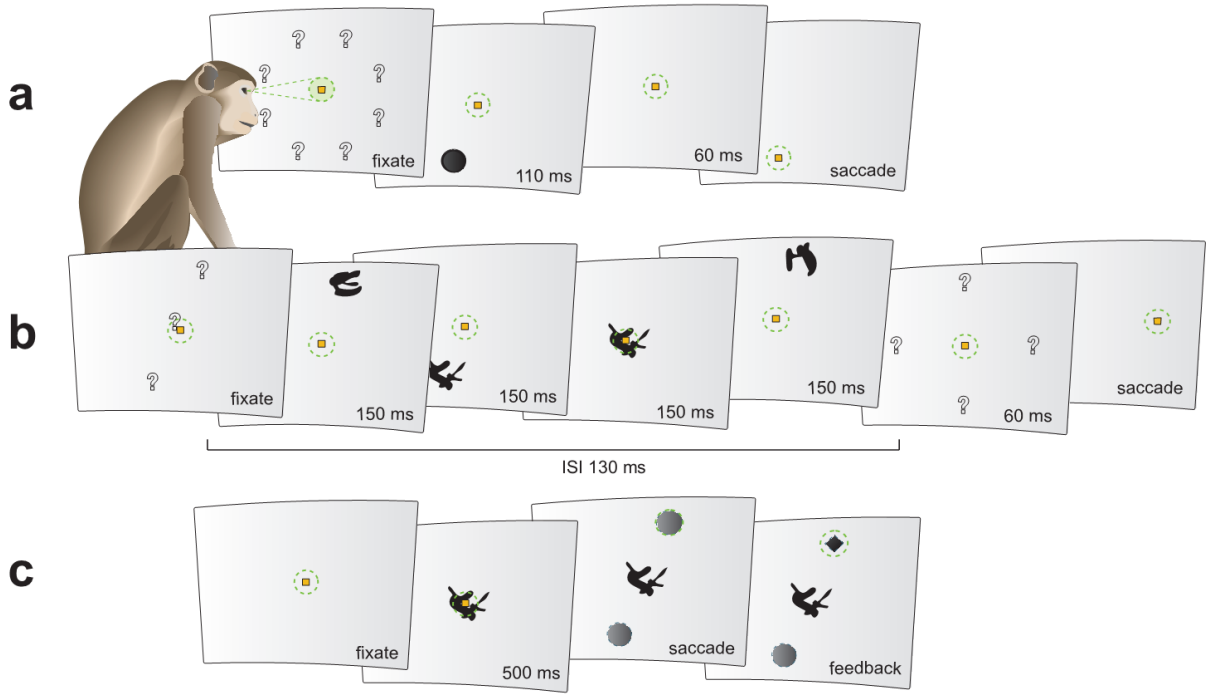

Figure 2.1. The three consecutive behavioral tasks. The approximate position of gaze is marked with a green dotted circle. Possible locations of upcoming stimuli are indicated by question marks. Neither the green dotted circle nor the question marks were actually present. **A,** Location selectivity mapping of eight peripheral locations equidistant from the center used to determine preferred (PREF) and anti-preferred (ANTI) locations. **B,** Passive shape-mapping task probing responses to visually presented shapes in the PREF, CENTER, and ANTI locations. **C,** Active shape-saccade association task where a centrally presented shape serves as a cue for saccading to the PREF or ANTI location.

Each trial of the passive shape-mapping task consisted of four rapid serial visual presentations (RSVPs) where black shapes (diameter approximately 3°; see figure 2.2) were flashed on a light gray background for 150 ms, with an inter-stimulus interval of 130 ms, in three possible locations: CENTER (7° eccentricity), PREF, and ANTI (7° eccentricity), as determined

by online spike recordings from the location selectivity mapping task. The monkeys' eye position had to stay within 4° of the center of the screen.[1] The trials thus always aborted if the monkeys looked to the PREF or ANTI locations. A yellow fixation square (side length 0.3°) was shown in the center of the screen. 60 ms after the disappearance of the last shape, the fixation square jumped to one of four possible locations randomly picked to be up, down, right, or left of the center (6° eccentricity). These target locations never overlapped with the PREF or ANTI locations. The monkeys were rewarded for making a saccade to the new location of the square.

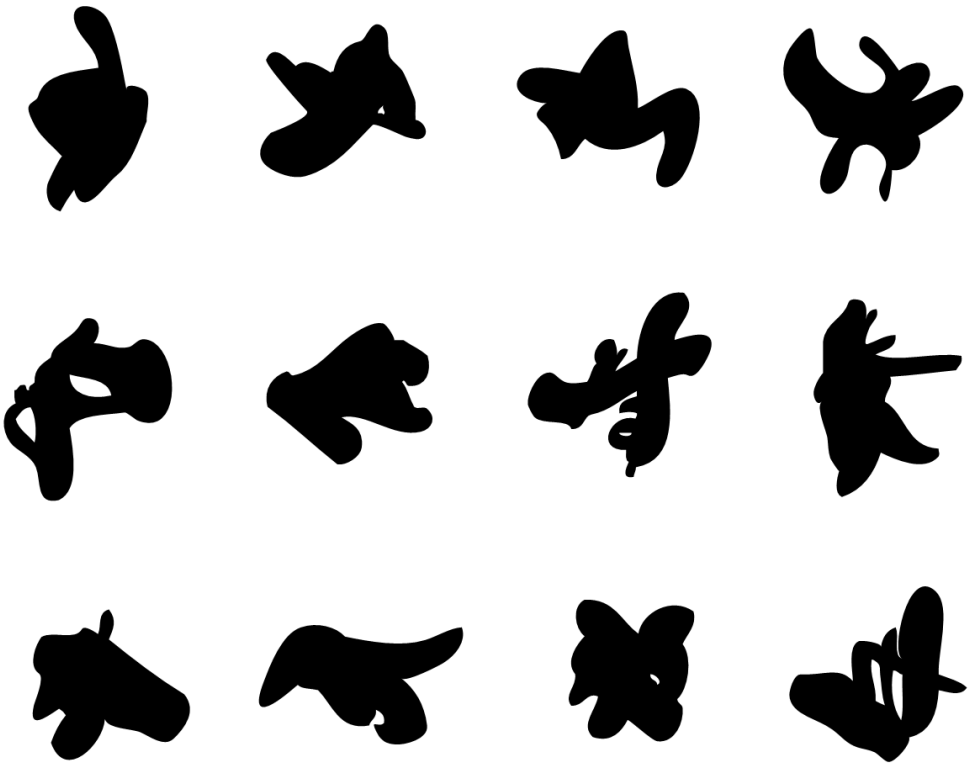

Figure 2.2. Example shapes. The shapes are not shown to scale.

[1] We fully acknowledge that this large window is not optimal for some of the analyses reported in this paper. One of the main findings from the passive shape-mapping task, i.e. that neural responses to novel shapes predict future orienting behavior, was unforeseen and the task was not specifically tailored to looking at such a relationship. Even the main behavioral effect, i.e. that there are apparent predispositions to associate objects of certain shapes with specific looking patterns, had never been previously reported. Several related behavioral experiments, described in chapter 3, confirmed that objects indeed are not neutral before they are associated with some action. Information derived from the shape of novel objects is integrated into a variety of processes, such as the allocation of visual attention, the programming of eye movements, and the perception of motion. Here, novel behavioral effects were predicted based on the current neurophysiological data. Had these effects not been found in people, it would have cast doubts on the generality of the neurophysiological findings.

For the passive shape-mapping task, a shape and a location were chosen pseudorandomly for each presentation, so that all shapes were shown equally often in all three locations. A total of eight different shapes were shown during a recording session. In most recording sessions, each shape appeared 20 times in each location. Four of the shapes were highly familiar to each monkey because he had been previously trained over the course of months to associate them with particular locations during the shape-saccade association task, as explained in more detail below. In each session we also showed four novel shapes which the monkey had never seen before and therefore had no particular associations. All shapes, familiar and novel, were originally generated by randomly selecting and overlapping four black strokes or pieces out of a set of 64, and then scaling them so that all composite shapes had the same area. Randomly generated sample shapes can be seen in figure 2.2.

The final task was an active shape-saccade association task where the eight shapes previously seen in the passive shape-mapping task now served as central precues, cueing the monkey to saccade either to the PREF or the ANTI location after a brief delay. Two of the novel shapes were randomly chosen to cue the PREF location and the other two cued the ANTI location. The same was true for the four familiar shapes, except that their associations were randomly chosen at the start of the monkey's training and this initial assignment to a location was maintained for the entire training and recording period. Each monkey trained on four sets of familiar shapes with four shapes in each, so they were highly familiar with 16 shapes which were different for the two monkeys. In each recording session, a set of familiar shapes was chosen to match the PREF and ANTI locations of the neuron being recorded from. The active shape-saccade association task was run in blocks for 96 trials each. The first block had equal numbers of novel and familiar shapes. Provided that the monkeys were willing to complete further trials, this first mixed block was in most cases followed by three blocks of trials where only novel shapes were shown in order to provide more experience with novel shapes. These novel blocks were followed by mixed blocks, again provided that the monkeys were willing to work. Our analysis will mostly focus on the first block of trials.

A trial started with the appearance of a central fixation square (side length 0.3°). After the monkey acquired fixation, one of the shapes from the previous passive shape-mapping task was randomly chosen to appear in the center of the screen and was visible for the remainder of the trial. The monkey was required to keep fixating within 1° of the screen center for 500 ms (shape

period), after which the fixation square disappeared and two identical gray choice disks (radius 1°) appeared, one in the PREF location and the other in the ANTI location (choice period). The monkey was then free to break fixation by saccading to one of the two choice disks. The shape served as a 100% valid central precue so it determined what was considered the correct choice. The monkey received visual and auditory feedback for his choice; a correct choice was followed by a low-pitched tone and the chosen disk was substituted by a black diamond, while an incorrect choice was followed by a high-pitched tone and the disappearance of the chosen disk.

Cell Recording and Selection

Recorded action potentials were sorted offline using the WaveClus spike clustering algorithm (Quiroga, Nadasdy, & Ben-Shaul, 2004). From this we identified a total of 117 units, 82 of which were suitable for further analysis (monkey J: N=44, monkey R: N=38). We included cells that met the following criteria: a) the assumed PREF and ANTI locations, as determined by online spikes from the location selectivity mapping task, corresponded to the actual PREF and ANTI locations, as determined by offline analysis, b) firing rate for centrally presented shapes remained high enough for the maximum depth of selectivity index to be calculated (see Results), c) the monkeys completed all necessary tasks, i.e. the location selectivity mapping task, the passive shape-mapping task, and more than one block of the shape-saccade association task.

Data Analysis

Unless otherwise noted, all statistical tests were two-sided and had an alpha level of 0.05. For repeated measures ANOVAs, results were Greenhouse-Geisser corrected if Mauchly's test of sphericity was significant.

When analyzing data from the passive shape-mapping and active shape-saccade association tasks, we aligned neural responses in every trial to the visual onset of each shape and counted the number of action potentials within a 50 ms window centered on the time of onset. We repeated this process for windows spaced 10 ms apart. Unless otherwise stated, any reference to timing in the following text indicates the center time of such a window.

Results

Selectivity

As previously described, data from the location selectivity mapping task was used to define a preferred location of each LIP unit. Most units had a preferred location in the contralateral hemifield (67 CONTRA units) while a minority preferred a location in the ipsilateral hemifield (15 IPSI units). The circular mean direction of the preferred location was 192°, and the circular standard deviation was 59.7°.

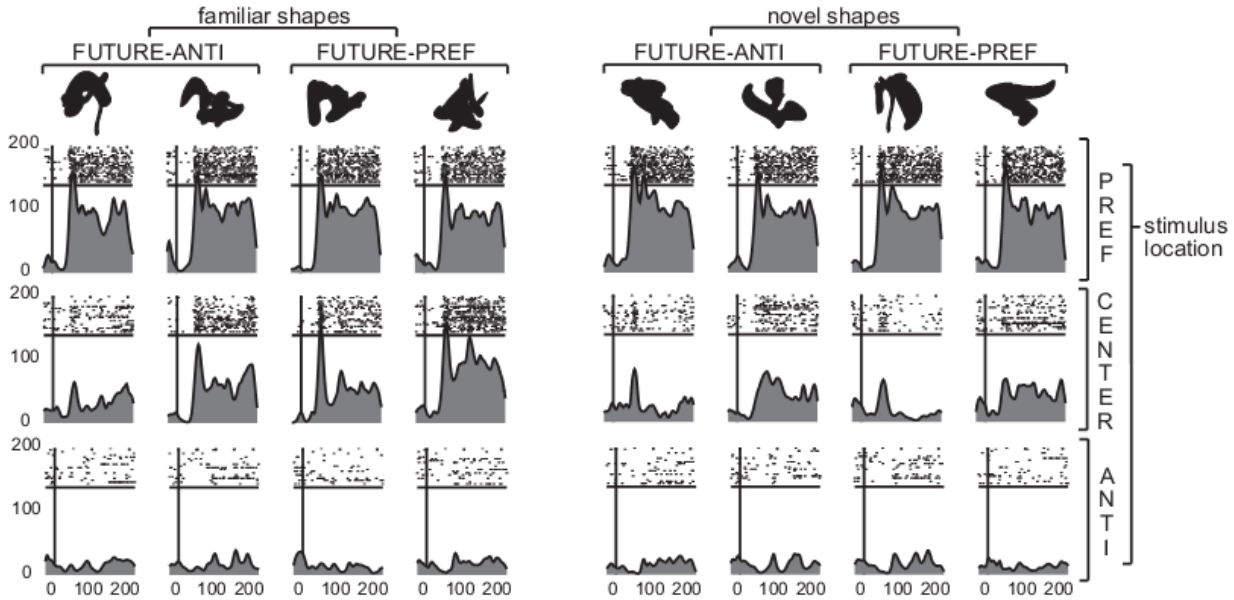

Figure 2.3. Example neural responses in the passive shape shape-mapping task. These spike density functions show one unit's responses to familiar and novel shapes shown in the preferred (PREF) location, the center of the screen (CENTER), and the anti-preferred (ANTI) location. In the following active shape-saccade association task, the FUTURE-ANTI shapes served as 100% valid central precues to the anti-preferred location, and the FUTURE-PREF served as such cues to the preferred location.

In the passive shape-mapping task, more CONTRA units also showed greater responses for shapes presented contralaterally than ispilaterally, and vice versa for IPSI units. One-sample binomial tests at times 0 to 190 ms after visual onset of shapes in the passive task confirmed that more units kept their location preference (contralateral versus ipsilateral) across these two tasks than would be expected by chance (CONTRA units: significant at all times from 30 to 190 ms

after shape onset, all ps < 0.001; IPSI units: significant from times 30 to 80 ms after shape onset, first p = 0.035, all other ps < 0.008). Figure 2.3 shows an example unit's responses to shapes shown in different locations.

LIP units seemed to range greatly in their passive responses to visually presented shapes. Some units differentially responded to shapes in more than one location, others showed such shape selectivity mainly in a single location, and yet others showed little selectivity for the shape of passively viewed stimuli. We wanted to quantify this shape selectivity and test whether shape selectivity was cell-specific and location-specific. Furthermore, we wanted to know if and then how much passive shape selectivity was affected by experience in the active shape-saccade association task. For each neuron and for each location (PREF, CENTER, and ANTI), we calculated a depth of shape selectivity (DoS) in the passive shape-mapping task (Rainer & Miller, 2000):

$$DoS = \frac{n - \frac{\sum R_i}{R_{max}}}{n - 1}$$

DoS can range from 0 (cell responds equally to all shapes) to 1 (cell responds only to one shape). LIP responses are often brief and dynamic, so shape selectivity and preference can change over a short period of time. We therefore calculated a DoS for each time window centered on 40 ms after visual onset to 190 ms after shape onset (or, equivalently, 40 ms after visual offset), and used the maximum DoS index as a measure of the neuron's shape selectivity. We did this separately for familiar and novel shapes, and separately for shapes presented in the PREF, CENTER, and ANTI locations. Note that for five units, the maximum DoS for the ANTI location could not be defined because of low firing rate. From here on, we will use the term *shape selectivity* when referring to the maximum DoS.

Shape selectivity was significantly positively correlated across all combinations (15 total) of location (PREF, CENTER, and ANTI) and stimulus type (familiar and novel). All correlations can be seen in figure 2.4, see also figure 2.5. These positive correlation coefficients imply that the shape selectivity measures capture a property of the neurons themselves. Within each location, the shape selectivity for familiar and novel shapes is highly correlated (r >= 0.75). The correlation between shape selectivity in the center and the anti-preferred location is also fairly

strong (CENTER vs. ANTI: r >= 0.55) indicating that a unit with relatively high shape selectivity in the ANTI location is likely to have a relatively high shape selectivity in the CENTER. Shape selectivity in the preferred location, on the other hand, appears to be somewhat special. While it is significantly positively correlated with shape selectivity in the other two locations, the correlation coefficients tend to be lower (PREF vs. CENTER: r >= 0.34; PREF vs. ANTI: r >= 0.28).

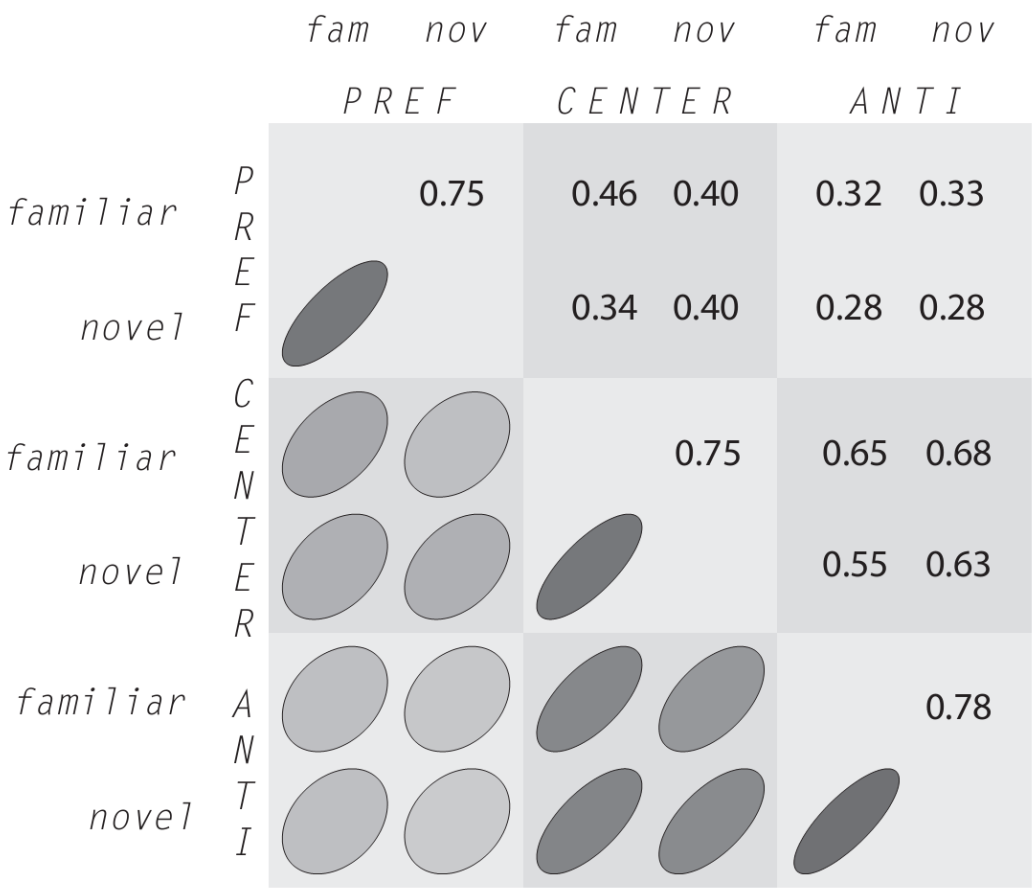

Figure 2.4. Shape selectivity correlation matrix. This matrix shows the relationship between the shape selectivity of LIP neurons as defined by their responses to either familiar or novel shapes and in three different locations (the preferred location, the center, and the anti-preferred location of each unit). Numbers indicate Pearson's r. Ellipses are the contours of a bivariate normal distribution with a correlation r (Murdoch & Chow, 1996).

A principal components analysis (rotation: Varimax; extraction of components with an Eigenvalue greater than 1) confirmed that shape selectivity in the preferred location is somewhat different from shape selectivity as measured in the other two locations. We reduced the six

measures of shape selectivity (for familiar and novel shapes in three different locations) to two components (explained variance: 49% and 30%, respectively). All the six original shape selectivity variables loaded positively on the two factors. The loadings on the first factors were still much higher for the ANTI and CENTER shape selectivity measures (loadings >= 0.79) than it was for the PREF shape selectivity measures (loadings <= 0.24). The reverse was true for the second factor where the loadings for PREF shape selectivity measures were much higher (loadings >= 0.89) than for shape selectivity in the other two locations (loadings <= 0.25). The shape selectivity of LIP neurons might therefore consist of two components: One which gets a greater weight in the preferred location of the neuron, and another which gets a greater weight outside of that preferred location.

We then performed a 2 x 3 repeated measures ANOVA with shape selectivity as a dependent measure and stimulus type (familiar or novel) and location (PREF, CENTER, or ANTI) as the independent factors. The selectivity for familiar shapes (M = 0.516) was significantly greater than that for novel shapes (M = 0.496; $F(1,76) = 5.315$, $p = 0.024$). Shape selectivity also significantly varied by location ($M_{PREF} = 0.421$, $M_{CENTER} = 0.556$, $M_{ANTI} = 0.541$; $F(2,152) = 34.606$, $p = 4.1 \times 10^{-13}$). Follow-up t-tests showed that the shape selectivity of the CENTER and ANTI locations did not significantly differ from each other (familiar shape selectivity: $t(76) = 1.407$, $p = 0.163$; novel shape selectivity: $t(76) = 0.387$, $p = 0.700$), but their shape selectivity was significantly greater than in the PREF location (shape selectivity for familiar PREF vs. familiar CENTER, familiar PREF vs. familiar ANTI, novel PREF vs. novel CENTER, and novel PREF vs. novel ANTI, all $ps < 5.0 \times 10^{-6}$). We did not detect a significant interaction between stimulus set and location ($F(2,152) = 0.763$, $p = 0.468$). We do note that the selectivity for familiar shapes is only significantly greater than for novel shapes in the central location (see figure 2.5) where the familiar shapes had been repeatedly presented in the active shape-saccade association task (PREF: $t(81) = 0.853$, $p = 0.396$; CENTER: $t(81) = 2.183$, $p = 0.032$; ANTI: $t(76) = 1.236$, $p = 0.220$).

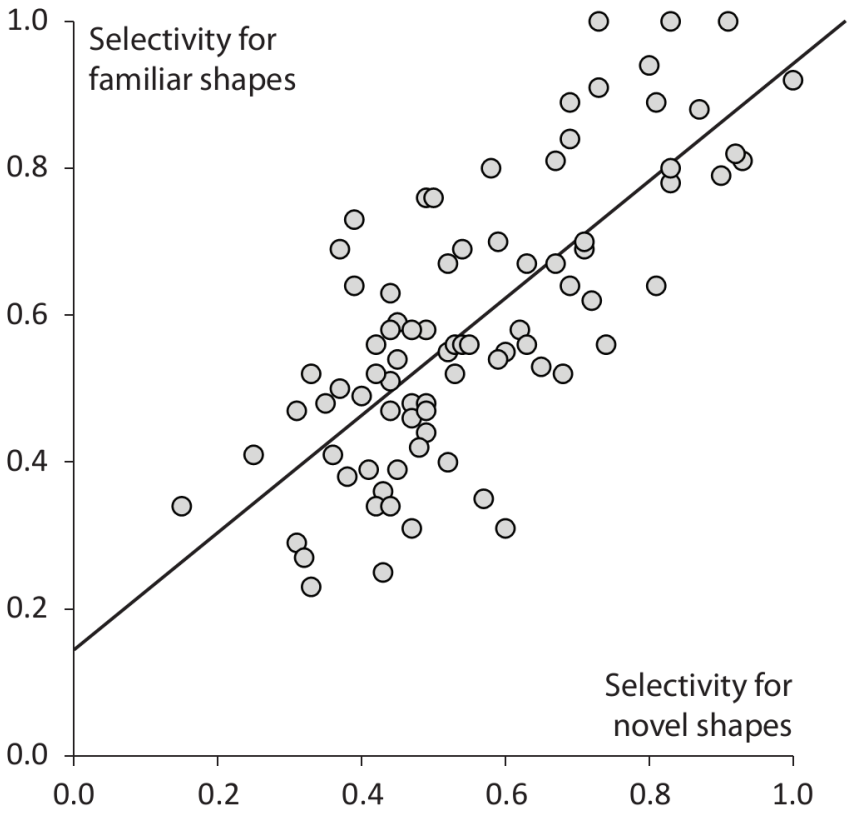

Figure 2.5. Relationship between the selectivity for familiar and novel shapes shown in the CENTER location. Each marker corresponds to one LIP unit. The line shows the linear least squares fit.

To summarize, the selectivity of responses to visually presented shapes varies greatly across cells, where some LIP neurons are consistently more shape selective than others. Shape selectivity is highly dependent on location and is much greater outside of the neurons' preferred spatial position. Shape selectivity is enhanced through experience and, although the data on this is not definitive, this enhancement might be greatest in the center location where the familiar shapes had most often been seen and had been relevant for past behavior.

Shape Responses Predict Future Orienting Actions

The first block of the active shape-saccade association task had an equal number of trials showing novel shapes and familiar shapes. The monkeys' performance for familiar shapes was in general very good or 92% on average in 73 sessions. If the monkeys were randomly executing saccades to the PREF and ANTI locations on novel shape trials then they would be expected to make the correct choice on half of those trials. In reality their accuracy ranged from 29% to 90%

with a mean performance of 54%. While their performance was significantly better than expected based on chance alone ($t(73) = 3.355$, $p = 0.001$, one-sample t-test), it was still on average very close to chance with a wide performance range. This performance range was greater than would be expected had the monkeys guessed randomly (Levene's test of equal variances in the percent correct for novel shapes and an equally large sample of simulated binary choices: $F=27.447$, $p = 1.0 \times 10^{-6}$).

For unknown reasons, learning arbitrary associations between a shape and a saccade in general proved to be difficult, and while the monkeys sometimes did quite well, other times their performance was considerably worse than expected from mere random guesses. We reasoned that the monkeys' performance was being influenced by the shape of the cues that they had to learn. The shape of the novel stimuli might directly influence the monkeys' performance by inducing an orienting bias, effectively pushing them toward or pulling them away from the correct choice location.

We wanted to know whether LIP shape selectivity might be the source of such a shape-induced orienting bias. If LIP responses to novel shapes bias orienting, then that bias can either be congruent or incongruent with a shape's future association in the active shape-saccade association task. When an LIP neuron responds vigorously to a shape in the passive task, and the monkey later learns that when he sees that shape he should saccade toward the neuron's preferred location, then the neural shape responses are *congruent* with the association. If, however, the monkey has to learn that the shape is associated with the opposite location, the neural responses are *incongruent*.

For the passive shape-mapping task, we compared the distributions of each neuron's firing rates for the two novel shapes which would later cue the PREF location, and the other two novel shapes which would later serve as cues to the ANTI location (from now on referred to as FUTURE-PREF and FUTURE-ANTI shapes, respectively). More specifically, for every time window between 0 and 190 ms after shape onset, we calculated the area under the receiver operating characteristic curve (AUC) comparing these two distributions (Green & Swets, 1966). We then scaled the AUC scores so that they could theoretically range from -100 to 100. In the rest of the paper we will refer to the scaled score as *congruency*:

$$congruency = 200 \times (\mathrm{AUC}_{\mathrm{FUTURE-PREF\ over\ FUTURE-ANTI}} - 0.5)$$

A positive congruency score implies that in general the neural responses to FUTURE-PREF shapes were higher than to FUTURE-ANTI shapes, i.e. the responses were congruent with the future associations of the shapes. The reverse is true for a negative score; it represents incongruent activation. The greater the absolute value of a score, the greater was the separation between the neural response distributions of FUTURE-PREF and FUTURE-ANTI shapes. We finally correlated congruency values with accuracy, or percent correct, for those same shapes in the first block of the active shape-saccade association task that immediately followed the passive task.

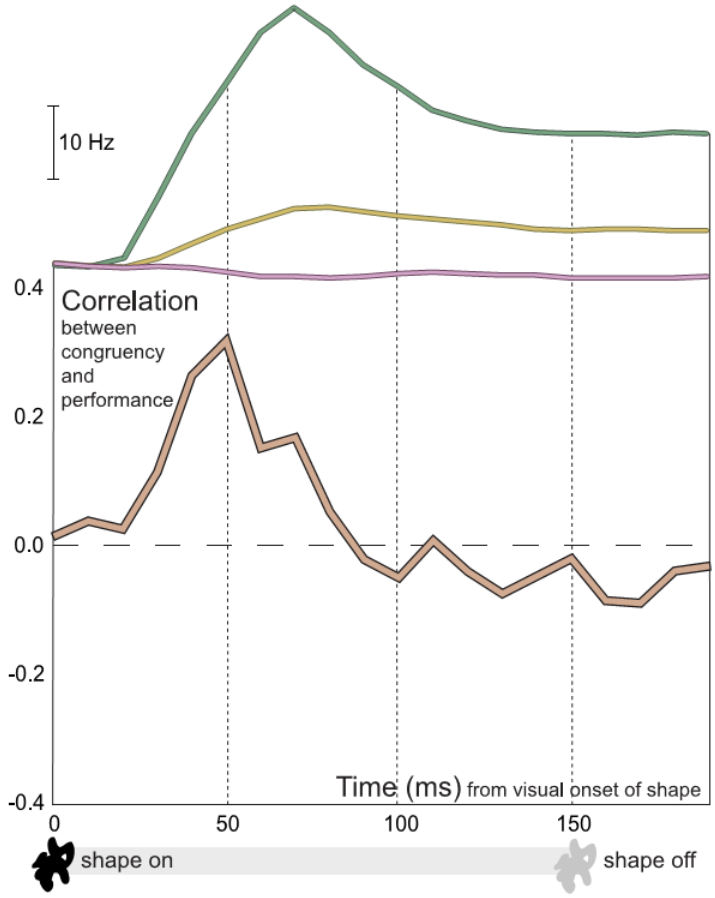

Figure 2.6. Fast passive responses to novel to-be-learned shapes predict future behavioral performance. The main graph (in brown) shows the Pearson's correlation (y-axis) between neural congruency scores for novel shapes at different time points in the passive shape-mapping task (x-axis) and behavioral performance in the active shape-saccade association task on trials where those same shapes were used as central precues. The aligned upper graph shows the mean responses across neurons, in sliding 50 ms time bins, for novel shapes presented in the PREF (green), CENTER (yellow), and ANTI (pink) locations in the passive shape-mapping task.

We found that congruency scores based on responses to novel shapes in the passive shape-mapping task were significantly correlated with performance on novel shape trials in the active shape-saccade association task (figure 2.6). The correlation peaked 50 ms after shape onset (r = 0.32, p = 0.003).

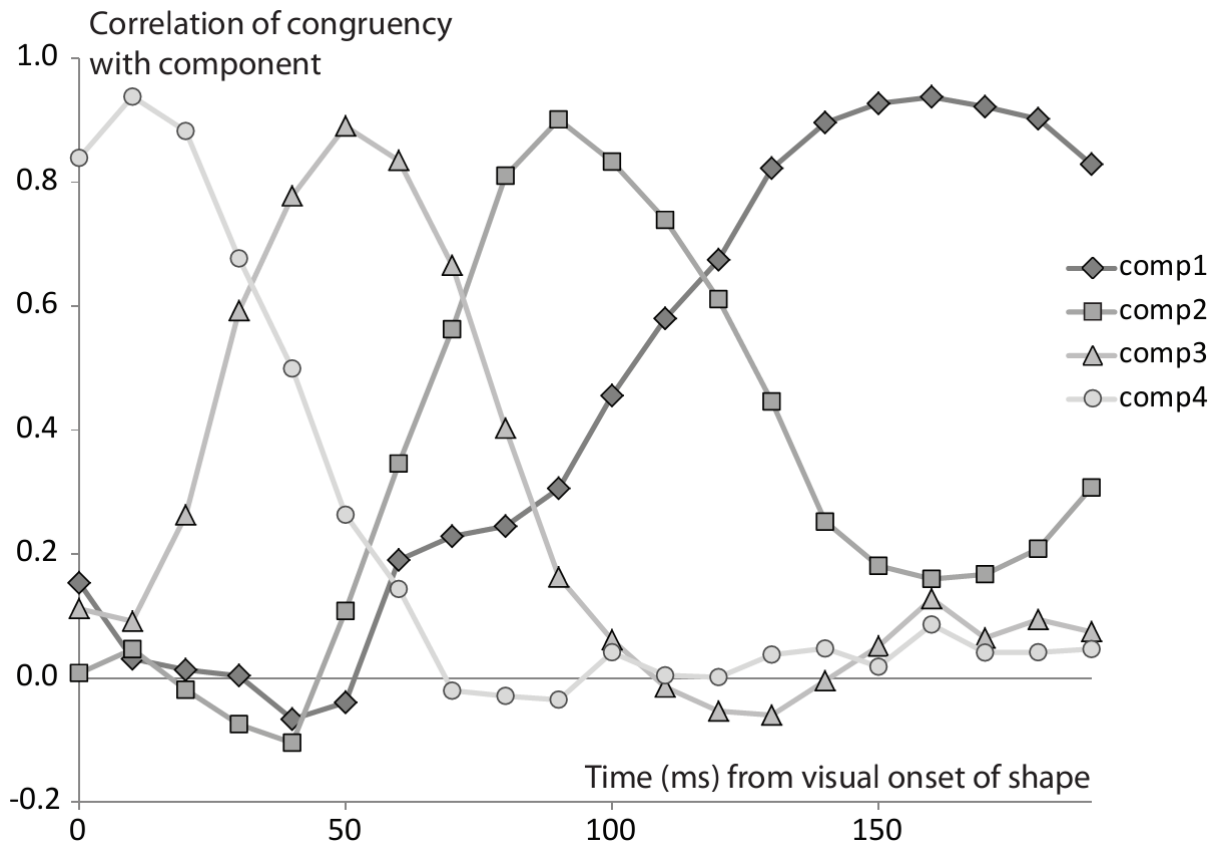

Figure 2.7. Correlation of congruency scores with four extracted principal components. We reduced 20 congruency scores from the passive shape-mapping task, one score for each time point, to four principal components. A strong correlation with a component indicates that the congruency scores from that particular time point contribute greatly to the component scores.

The 20 correlation coefficients are not independent of each other; each neuron's congruency scores are based on neural activity in partially overlapping time bins. This partial dependence complicates interpretations of statistical significance. In order to get around this problem, we performed a principal components analysis to reduce the 20 time variables down to fewer dimensions that are uncorrelated with each other. Each time variable consisted of 82 measures of the congruency of responses to novel shapes, one for each unit. Four components

were extracted (eigenvalues > 1); together they explained 86.5% of the variance of the original variables. The four components of the rotated solution (method: Varimax) explained 34.2%, 20.2%, 16.1%, and 15.9% of the total variance, respectively. The correlations of the original time variables with the components are shown in figure 2.7.

The first, second, and fourth principal components are not significantly correlated with performance on novel shape trials in the active shape-saccade association task (first: $r(80) = -0.06$, second: $r(80) = -0.03$, fourth: $r(80) = 0.00$, all ps > 0.56). The third component, which corresponds mostly to congruency of the earliest passive LIP responses to novel shapes, is significantly correlated with performance ($r(80)=0.28$, $p=0.01245$; threshold for significance with Bonferroni correction: 0.0125).

Thus, rapid, passive responses to novel to-be-learned shapes predict future performance in the active shape-saccade association task. When early neural responses in the passive shape-mapping task were congruent with the future association or rule, the monkeys were more likely to choose the correct location in response to seeing those shapes in the active shape-saccade association task.

We suspected this correlation to be mainly driven by neurons with higher shape selectivity in the center location where the shapes were then shown in the active shape-saccade association task; neurons responding similarly to all the shapes are by definition not very informative. To see if the relationship between congruency and behavior significantly increased with greater shape selectivity, we regressed accuracy (percent correct in the active shape-saccade association task) against congruency (for novel shapes at 50 ms in the passive shape-mapping task), shape selectivity (as defined by central novel shapes in the passive shape-mapping task), and an early congruency×shape selectivity interaction term, which is of most interest for our question. The conditional effects of congruency (Beta = -0.44, $p = 0.199$) and shape selectivity (Beta = -0.12, $p = 0.251$) did not reach significance, while the congruency×shape selectivity interaction was significant (Beta = 0.809, $p = 0.020$).

This significant interaction indicates that the effect of congruency on behavioral performance is dependent on shape selectivity (figure 2.8). Ranking the units from the least to the most shape selective, the bottom one-third shows a correlation of $r(25) = 0.05$, the middle one-third has a correlation of $r(26) = 0.34$, and the top one-third of the units has a correlation of $r(25) = 0.62$.

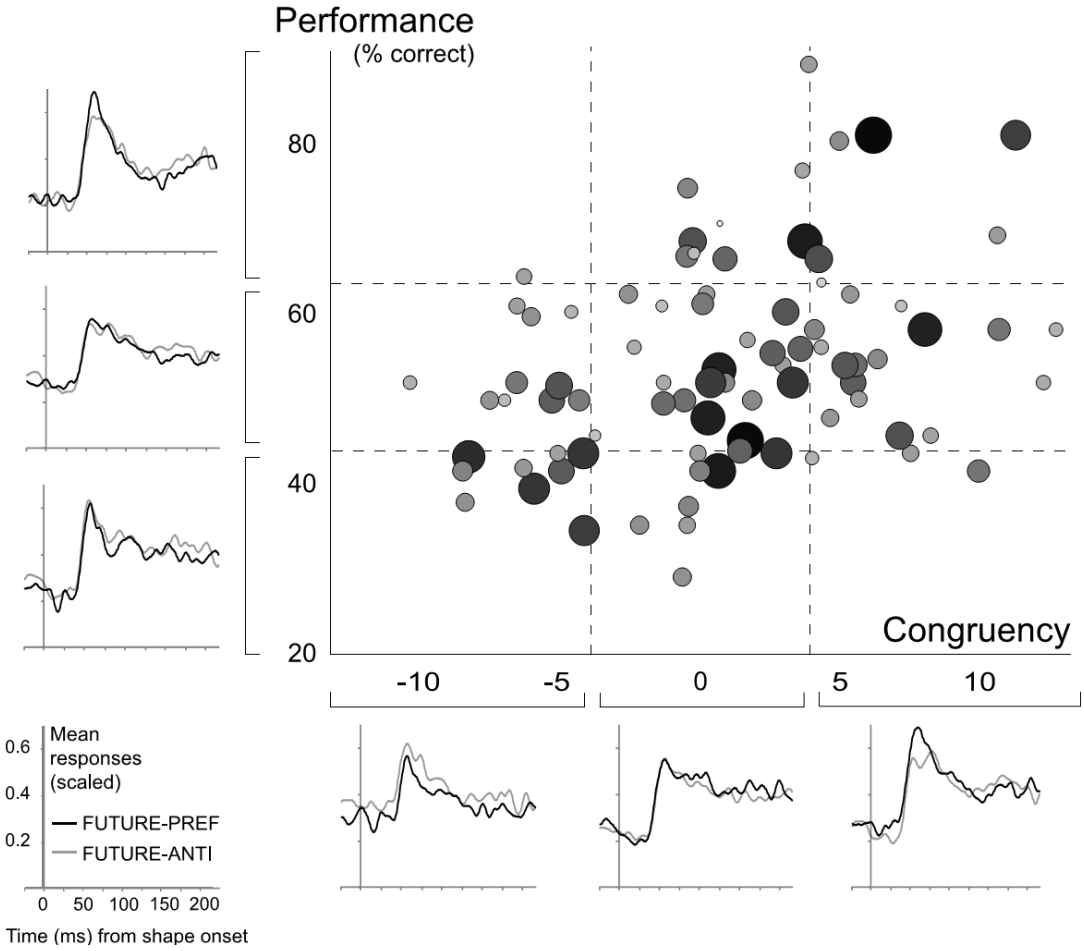

Figure 2.8. LIP neurons with higher selectivity for novel central shapes better predict future behavior. Each marker in the scatter plot corresponds to one unit, and larger and darker markers indicate greater shape selectivity. The x-axis shows the congruency of responses to novel shapes at time 50 ms after shape onset in the passive shape-mapping task. The y-axis shows the percent correct for the same shapes in the following active shape-saccade association task. The margins show the mean spike density functions (Gaussian kernel, 5 ms SD, 1 ms output resolution, responses scaled between minimum and maximum firing rate for each unit) for responses to FUTURE-PREF (dark gray) and FUTURE-ANTI (light gray) novel shapes in the passive shape-mapping task before behavioral performance data was collected. The left margin groups units based on behavioral performance and the bottom margin groups them based on neural congruency.

The neural responses which most strongly predicted later behavior occurred so early after the visual onset of our stimuli that they are clearly stimulus-driven; it is extremely unlikely – if not impossible – that they reflect feedback or an error signal from a motor command such as an

eye movement. The congruency scores were also calculated by using all trials, effectively collapsing across the retinotopic location of the shape presentations. Additionally, the passive shape-mapping task always aborted if the monkeys looked to the PREF or ANTI locations, and they were only rewarded if they followed a fixation jump to one of four possible locations which never overlapped with the locations of any shape stimuli.

Nevertheless, we reran some of our analysis using only spiking activity from the passive shape-mapping task where the monkeys' eye position stayed within 1.0 degrees of the fixation position from the visual onset of a shape until 75 ms after the offset of a shape. We compared this to randomly selecting the same number of trials from each session. We repeated this random selection 10 times. Both methods result in some data loss, but only the former method selects trials based on the monkeys' eye position. If selecting trials based on eye position gives results that are highly similar to those expected from random selection, then we would conclude that eye position is not a primary driver of our results.

The results were similar to our main analysis. The measures of the neurons' selectivity for novel shapes were virtually unchanged (correlation between uncorrected and eye position corrected data: r=0.98; correlation between uncorrected and randomly selected data: mean r=0.97, standard deviation=0.004). The same was true for selectivity for familiar shapes (correlation between uncorrected and eye position corrected data, r=0.96; correlation between uncorrected and randomly selected data: mean r=0.98, standard deviation=0.004). Shape selectivity for familiar shapes was still on average higher than selectivity for novel shapes (original data: familiar mean = 0.59, novel mean = 0.56; eye movement corrected data: familiar mean = 0.61, novel mean = 0.57; randomly selected data: familiar mean =0.60, novel mean = 0.58; familiar standard deviation = 0.004, novel standard deviation = 0.003). The earliest responses of the neural population to novel shapes in the passive shape-mapping task were most predictive of the monkey's behavioral performance in the active shape-saccade association task (correlation between percent correct and congruency at 50 ms after shape onset: original data r=0.32; eye position corrected data r=0.27; randomly selected data: mean r=0.28, standard deviation=0.05). The neurons with the highest shape selectivity for novel shapes were most highly predictive of future orienting actions (correlation between percent correct and congruency at 50 ms after shape onset for the least, medium, and most shape selective units, respectively; original data: r=0.05, r=0.34, r=0.62; eye position corrected data: r=0.10, r=0.22, r=0.53;

randomly selected data means: r=0.13, r=0.22, r=0.51; randomly selected data standard deviations: 0.11, 0.10, 0.06). We therefore conclude that our results are unlikely driven by possible differences in eye position.

Orienting Actions Affect Shape Responses

We wanted to see if and how the responses to novel shapes in the active shape-saccade association task changed with short-term learning, or learning over the course of a single session. We could then contrast these shorter-term learning effects with the effects of long-term learning over the course of days, weeks or months.

In order to look for changes across the day, we examined the responses to novel shapes in two blocks of the active shape-saccade association task: the first block in a session and the block with the best behavioral performance for novel shape cues in the same session, provided that the block included at least 30 novel shape trials and that the monkey showed any behavioral improvements after the first block (77 out of 82 units). Note that we refer to shape cues as novel as long as they have not been seen in previous sessions, and will use the terms *early* and *late* novel shape trials. To examine long-term learning effects, we compared neural responses to familiar shapes that in the past had been associated multiple times with either orienting to the PREF or ANTI location of the neuron recorded from. We did this both for the responses recorded in the passive shape-mapping task and in the first block of the active shape-saccade association task which immediately followed the passive mapping.

Specifically, we looked at the differences in the neural responses to shapes that cued the PREF and ANTI location by calculating the congruency scores for 50 ms wide windows every 10 ms from the visual onset of shape, as described in the previous session of the Results. This was done separately for responses to familiar shapes in the passive and active task, as well as for both early and late novel shape trials in the active task. Only correct trials of the active task were included, so in all cases the monkey eventually made an eye movement to the location cued by a central shape.

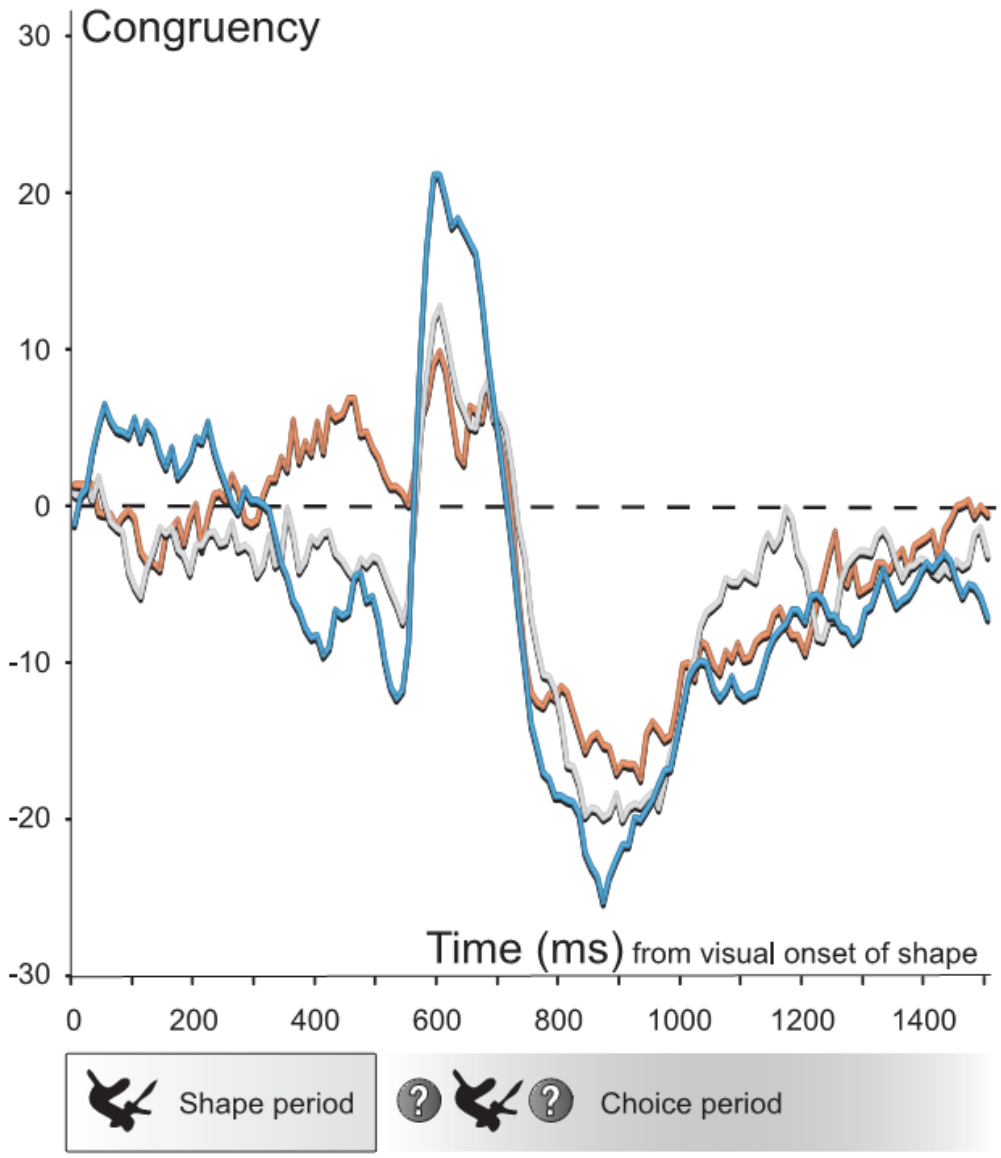

Figure 2.9. Congruency of the neural population responses systematically changed across a trial of the active shape-saccade association task. The mean congruency scores at each time after the visual onset of shape are shown for early novel (orange), late novel (gray), and familiar (blue) shape trials. A positive congruency score signifies that the firing rate was in general higher during PREF shape trials than ANTI shape trials, while a negative score indicates the opposite.

As can be seen in figure 2.9, congruency systematically changed across a trial of the active shape-saccade association task. We are mainly interested in the shape period, or the 500 ms time period between the visual onset of shapes and choice disks. To first briefly describe the neural dynamics in the following choice period, the responses of the neural population in all

cases became congruent almost immediately after the visual onset of the choice disks, sharply became incongruent around 160 ms later, and finally leveled off. This was most apparent for familiar shape trials and least apparent for early novel shape trials even though the monkeys' overt behavioral choices were equated. Within a single session of learning where to orient in response to seeing a novel shape, the population response dynamics during the choice period started to resemble those of the familiar over-learned shape trials.

We wanted to know whether and then how shape responses were affected by short- and long-term learning of associating shapes with orienting to either a neurons' preferred or anti-preferred location. We started by looking at the response dynamics within the shape period of the active shape-saccade association task for early novel, late novel, and familiar shape trials. We first ran three separate repeated measures ANOVAs with time as the single factor. The time variable consisted of congruency scores for 10 non-overlapping 50 ms time bins centered on 50 to 500 ms after stimulus onset. Congruency did not significantly vary over time for early ($F(6.164,468.435) = 0.702$, $p = 0.652$) or late ($F(3.645, 277.008) = 0.533$, $p = 0.851$) novel shapes. Congruency did, however, vary over time for familiar shapes ($F(3.019, 229.414) = 5.345$, $p = 0.001$). Responses to familiar shapes were congruent right after visual onset but became increasingly incongruent as the start of the choice period drew nearer. This incongruency might reflect experience-dependent mechanisms that prevent the monkeys from looking ahead before the appearance of the choice disks.

We followed up with single sample t-tests at each time point and for each type of cue (early novel, late novel, and familiar) where we looked at whether the congruency scores were significantly different from zero (30 tests in total). Using conventional significance levels, the early novel responses were significantly congruent 450 ms after shape onset ($p = 0.032$; all other ps > 0.074), late novel responses were never significantly congruent or incongruent (all ps > 0.055), and responses to familiar shapes were significantly congruent 50 ms ($p = 0.0005$) and 100 ms ($p = 0.035$) after shape onset, and significantly incongruent 400 ms after shape onset ($p = 0.036$). Early neural responses (i.e. 50 ms after shape onset, $M = 6.8$, $SD = 16.8$) to familiar shapes were significantly congruent even when a stringent correction for multiple comparisons was applied (threshold of significance with Bonferroni correction: 0.0017).

The mean neural responses to novel shapes were not significantly congruent or incongruent at this time, neither in early novel shape trials ($M = -0.5$, $SD = 22.71$, one sample t-

test, $t(81) = -0.208$, $p = 0.836$) nor late novel shape trials ($M = 0.3$, $SD = 21.28$, one sample t-test, 80 cells, $t(76) = 0.128$, $p = 0.898$) of a learning session. Early responses to familiar shapes were significantly more congruent than those to both early (paired samples t-test, $t(81)=2.518$, $p=0.014$) and late (paired samples t-test, $t(76)=2.541$, $p=0.013$) novel shapes. Unlike for the novel shapes, the neurons showed characteristic response differences between familiar PREF and ANTI shape cues extremely early after the visual onset of the shapes. This difference was modest but robust; around twice as many neurons favored familiar shapes that cued their preferred rather than their anti-preferred location.

These early responses to familiar shapes tended to be congruent regardless of whether a unit's preferred location was contralateral or ipsilateral (congruency at 50 ms after shape onset for units with contralateral preference: $M=6.9$, $SD=17.37$; ipsilateral preference: $M=5.9$, $SD=14.49$; independent samples t-test for differences in means, $t(80)=0.214$, $p=0.831$). Units with contralateral preference would be exposed to the same visual stimuli as units with ipsilateral preference, but the shapes' meaning would differ; a shape associated with a contralateral unit's preferred location would be associated with an ipsilateral unit's anti-preferred location and vice versa. Early congruent responses are therefore unlikely to stem from some accidental properties of the shapes themselves, but instead reflect the learned task-related relationship between a shape and a neuron's spatial selectivity.

The responses to the same familiar shapes centrally presented in the passive task did not tend to show such a rapid distinction between shapes that in the past cued the PREF and ANTI location of the neuron recorded from ($M = 0.2$, $SD = 12.8$, one sample t-test, $t(81) = 0.119$, $p = 0.906$). At 50 ms after visual onset, congruency of the responses to familiar shapes was significantly greater in the active than the passive task (paired samples t-test, $t(81) = 3.556$, $p = 0.001$). The bottom-up shape responses of LIP neurons can therefore be task-dependent; information about learned associations of shapes is preferentially represented in the rapid responses of LIP neurons when that information is behaviorally relevant.

At a first glance, LIP responses to centrally presented shapes might seem little affected by the learning that took place within a single session. However, a neural population whose mean responses are neither congruent nor incongruent might nonetheless have gone through experience-dependent changes that are not reflected in the average congruency scores. In addition to looking at population averages, we therefore looked at whether congruency scores for

late novel shapes could be predicted based on congruency scores for familiar shapes over and above the prediction based on congruency scores for early novel shapes alone.

Specifically, we performed a hierarchical regression at each of the 10 time points in the shape period of the active shape-saccade association task. Congruency scores for late novel shapes were treated as a dependent variable. Congruency scores for early novel shapes and familiar shapes were entered as predictor variables in consecutive steps. We then looked at whether a model that included congruency scores of both early novel and familiar shapes predicted congruency scores for late novel shapes significantly better than a model where the congruency scores of early novel shapes were used as the sole predictor variable.

Congruency scores of early novel shapes alone significantly predicted congruency scores of late novel shapes at all time points in the shape period (minimum $R^2 = 0.081$, maximum $R^2 = 0.307$; all ps < 0.011). Adding congruency scores of the familiar shapes as a second independent variable significantly improved the predictive power of the statistical model at time 150 ms after shape onset (R^2 change = 0.042, p = 0.032) and then again at time 300 ms after shape onset and at all times from thereon (minimum R^2 change = 0.095, maximum R^2 change = 0.225; all ps < 0.004; threshold for significance after Bonferroni correction: 0.005). While the congruency scores of the late novel shapes kept some similarity to the congruency scores of the early novel shapes throughout the shape period, they increasingly resembled the congruency scores of the familiar shapes as the shape period progressed. Experience-dependent changes in LIP shape responses might therefore start to unfold over a relatively short period of learning although these changes are seen relatively late after the visual onset of an object.

Persistent Distinctive Shape-Related Activity after Long-Term Learning

We have shown that repeatedly associating visual shapes with orienting to particular locations can change how LIP neurons respond when those shapes are seen, so that even the earliest neural responses can reflect the orienting behavior to which the shapes have been linked. The question remains, then, to what extent the responses are overwritten by experience. Do responses to familiar shapes that cue the same location still retain some individual characteristics, even though the monkeys have been extensively trained on reacting to them in the same way?

Our experiment was set up so that two centrally presented familiar shapes cued each possible target location. We compared the neural responses of such same-meaning familiar

shapes to see if responses to shapes repeatedly linked to the same behavior were still distinct from one another. We did this by sliding a 50 ms window in 10 ms steps from 0 ms to 1500 ms after the visual shape onset in the first block of the active shape-saccade association task, counting the number of spikes within each window, and comparing the distribution of the number of spikes evoked by same-meaning shapes by calculating the area under the receiver operating characteristic curve (AUC) comparing these two distributions (Green & Swets, 1966). We did the same for responses from 0 ms to 190 ms after the onset of centrally presented familiar shapes in the passive shape-mapping task. Since we had no specific predictions about which of any two same-meaning shapes would evoke higher neural activity, we took the absolute value of the scaled AUC for each shape pair. For each time point we therefore found two such scores for each neuron, one comparing the response distributions of the two familiar PREF shapes and the other comparing the two familiar ANTI shapes, and defined the *distinction* score at each time point as the average of the two scores:

$$\begin{aligned} distinction \; &= 100 \\ &\times \Big(abs\big(\mathrm{AUC}_{\text{familiar PREF shape pair}} - 0.5\big) \\ &+ \; abs\big(\mathrm{AUC}_{\text{familiar ANTI shape pair}} - 0.5\big)\Big) \end{aligned}$$

This gave us a vector of distinction scores for each neuron that signified how well it differentiated among same-meaning shapes at each time point after the visual onset of shape in a particular task. The population means of the distinction scores at each time point in the active shape-saccade association task can be seen in figure 2.10.

The distinction scores can theoretically range from 0 to 100, where 0 indicates that the neural responses to same-meaning familiar over-learned shapes are indistinguishable, while 100 signifies that they are completely separable. In reality, the neural responses to two same-meaning shapes will almost always be somewhat different by chance alone. In light of our previous results, we wanted to know whether there were differences in the early shape responses to familiar shapes even though they had repeatedly been associated with the same orienting action.

We performed a one-sided permutation test to see whether distinction scores for same-meaning familiar shapes were significantly greater than expected by chance alone. For each

shape pair, we shuffled the labels (shape A or B) of the responses in all familiar shape trials and calculated a vector of distinction scores based on the shuffled labels. We did this separately for trials in the passive shape-mapping task and the active shape-saccade association task, and repeated the process 1000 times. Figure 2.10 then shows the distribution of shuffled distinction scores at each time point after shape onset in the active shape-saccade association task. The graph depicts how much LIP neurons tended to differentiate between same-meaning shapes at any given time.

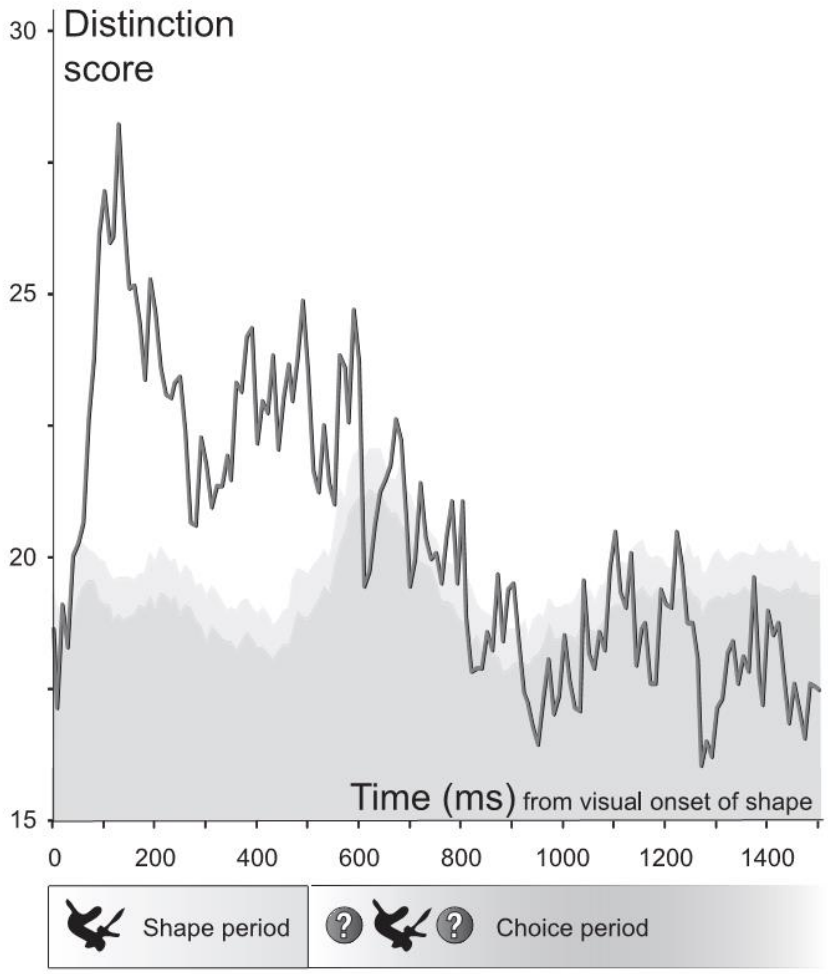

Figure 2.10. Distinction scores of familiar shapes in the active shape-saccade association task. Familiar shapes that have repeatedly been associated with the same arbitrary orienting action can still evoke differentiable neural responses. A permutation test showed that the mean distinction scores were significantly greater than expected by chance throughout almost the entire shape period (from 40 ms after shape onset and onward, excluding the time window centered at 50 ms after visual onset of shape). 95% of the permuted distinction scores fell within the dark gray band, and 99% within the light gray band.

The average distinction scores in the passive shape-mapping task first became significantly greater than expected by chance at 40 ms after visual shape onset ($p=0.031$). They stayed significant throughout the rest of the time periods tested (i.e. until 190 ms after visual onset, highest $p=0.011$, lowest $p<0.001$). The average distinction score in the active shape-saccade association task also first became significant 40 ms after visual onset ($p=0.026$), marginally missed the significance level at 50 ms after visual onset ($p=0.056$) and stayed significantly greater than expected by chance throughout the rest of the shape period (i.e. until 500 ms after visual onset, highest $p=0.044$, lowest $p<0.001$) and beyond.

The barely missed significance level at 50 ms in the active task is probably due to the fact that early responses to familiar shapes start to reflect their associated location or action in the task where these associations are relevant for behavior, as described above. At 50 ms, the original AUC scores for same-meaning shapes were nonetheless correlated across tasks (PREF shapes: $r(80) = 0.22$, $p = 0.043$; ANTI shapes: $r(80) = 0.24$, $p = 0.028$), indicating that the neurons in general kept their some of their selectivity to same-meaning shapes across tasks. Initial LIP shape responses probably have a task-dependent and a task-independent component.

Do the neurons that showed more distinctive responses to same-meaning shapes then not carry any information about the associated orienting action? In order to address this question, we divided the neural population into two subgroups based on distinction score at 50 ms after shape onset in the active shape-saccade association task (low difference score group, $N = 41$, difference score at 50 ms: $M = 12.6$, $SD = 4.30$; high difference score group, $N = 41$, difference score at 50 ms: $M = 29.2$, $SD = 8.72$). The response dynamics of the two subgroups were highly similar; they each showed the same characteristic repeated switchover of congruent and incongruent responses. The neurons that showed persistent distinctive shape-related activity therefore carried information about the associated orienting action at the same time.

Discussion

We find that rapid responses of LIP neurons to never-before-seen shapes predict future orienting behavior when those shapes are encountered again and should be acted on. We also find that rapid LIP shape responses reflect the orienting actions that in the past were associated with the shapes. Our results indicate that shape selective responses in LIP are closely tied to this

region's role in orienting.

LIP is interconnected with the frontal eye fields (FEF) and the anterior intraparietal area (AIP) which both have been found to be selectively responsive to the shape of at least some objects (Durand et al., 2007; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Peng, Sereno, Silva, Lehky, & Sereno, 2008; M. E. Sereno et al., 2002). LIP is also known to be interconnected with shape selective areas of the temporal lobe (Webster, Bachevalier, & Ungerleider, 1994) but visual onset latencies of neurons in those regions tend to be long (Baylis, Rolls, & Leonard, 1987; Kiani, Esteky, & Tanaka, 2005; Tamura & Tanaka, 2001). Nonetheless, some regions do have relatively short latencies. For example, area TEa in the superior temporal sulcus sends projections to LIP (Blatt, Andersen, & Stoner, 2004) and at least some neurons there have short visual latencies (Baylis et al., 1987). V4 is another candidate primary input region. It is tuned to shape features (Kobatake & Tanaka, 1994) and has known feedforward connections to LIP (Blatt et al., 2004; Ungerleider, Galkin, Desimone, & Gattass, 2008). These connections, however, are mainly from the V4 peripheral field representations (Ungerleider et al., 2008), and even though some V4 neurons have been reported to have visual latencies on the order of around 50-60 ms (Lee, Williford, & Maunsell, 2007), the majority appears to respond with much longer latencies (Schmolesky et al., 1998).

Here we find that orienting-related shape responses in LIP appear so early after visual onset that it is highly unlikely that they are the result of feedback from other shape selective areas, nor are they likely the result of feedback from motor commands. Instead these responses appear to be generated from the initial bottom-up wave of visual signals that reach LIP. It is possible or even likely that LIP shape selectivity is not solely inherited from ventral visual regions but is created *de novo* in the parietal cortex from yet unknown inputs. Even though it is doubtful that shape information reaches LIP solely through a circuitous route through the temporal cortex, we do consider it likely that LIP eventually receives some information about visual objects from the temporal cortex.

The earliest, apparently visual responses of LIP neurons can carry information about well-established yet still arbitrary associations of shapes with particular orienting actions, and later shape responses are affected by shorter-term learning of novel arbitrary visuomotor mappings. Several brain regions have been implicated in the acquisition and retainment of such arbitrary visuomotor associations (for reviews, see e.g. Brasted & Wise, 2004; Graybiel, 2005;

Fadila Hadj-Bouziane, Meunier, & Boussaoud, 2003; Murray, Bussey, & Wise, 2000; Passingham, Toni, & Rushworth, 2000; Seger, 2009; Wise & Murray, 2000). The premotor cortex – including the supplementary eye fields – (Brasted & Wise, 2004; Chen & Wise, 1995a, 1995b), the prefrontal cortex – including the frontal eye fields – (Asaad, Rainer, & Miller, 1998; Bussey, Wise, & Murray, 2001; Chen & Wise, 1995b; Pasupathy & Miller, 2005), the medial temporal lobe (Brasted, Bussey, Murray, & Wise, 2003; Mattfeld & Stark, 2011; Murray & Wise, 1996), and the basal ganglia (Brasted & Wise, 2004; Hadj-Bouziane & Boussaoud, 2003; Pasupathy & Miller, 2005; C.A. Seger, 2009; Tremblay, Hollerman, & Schultz, 1998; Williams & Eskandar, 2006) all might play a role in the initial learning of a new mapping between a stimulus and a response. Learning is also supported by dopaminergic reward prediction errors from midbrain structures (Bar-Gad, Morris, & Bergman, 2003; Tremblay et al., 1998). As learning progresses and the behavior becomes more automatic, other parts of the basal ganglia (Nixon, McDonald, Gough, Alexander, & Passingham, 2004; Seger, 2009) and the premotor cortex (Kurata & Hoffman, 1994; Nixon et al., 2004; Passingham, 1988) might start to take part in or even take over the representation of the overtrained associations. It has been argued that subcortical regions gradually train cortical areas on the associations so that eventually the behavior can be supported by the cortex (Pasupathy & Miller, 2005) although there have also been reports of simultaneous learning-related changes in neuronal activity in cortical and subcortical structures (Brasted & Wise, 2004).

The role of the parietal cortex in arbitrary visuomotor mapping is somewhat controversial. Functional neuroimaging studies have reported that neural activity in the parietal cortex can be affected by associative learning that happens over the course of a single session (Deiber et al., 1997; Eliassen, Souza, & Sanes, 2003), and that the parietal cortex can become progressively more involved as the arbitrary associations become increasingly automatic and overtrained (Eliassen et al., 2003; Grol, de Lange, Verstraten, Passingham, & Toni, 2006). Removing parts of the parietal cortex however does not seem to affect the learning of new associations or the retention of familiar ones (Pisella et al., 2000; Rushworth, Nixon, & Passingham, 1997). As an example, even though LIP neurons can become sensitive to colors if they have been arbitrarily associated with certain behaviors (Toth & Assad, 2002), monkeys do not have particular problems with relearning a similar task after parietal lesions, including a lesion of the lateral intraparietal area (Rushworth et al., 1997).

Brain areas other than the posterior parietal cortex might thus be responsible for the learning of a new arbitrary mapping between seeing a shape and saccading to a particular location. As learning progresses, the responses of LIP neurons to the novel shapes increasingly resemble activity seen for familiar shapes that share their meaning (i.e. cue the same location) although this happens relatively late after visual onset. This information is not related in any obvious way to the responses evoked by the presentation of visual stimuli in the preferred or anti-preferred locations of LIP neurons; it might be independent of the neurons' spatial selectivity and could be considered akin to the categorical information that has been previously reported to exist in LIP (Fitzgerald, Freedman, & Assad, 2011; Freedman & Assad, 2006, 2009). Such late categorical information could be fed back to LIP from other regions such as the prefrontal cortex which is thought to play a critical role in the classification of objects and events (Merchant, Crowe, Robertson, Fortes, & Georgopoulos, 2011; see Miller & D'Esposito, 2005 for a discussion on top-down control signals originating in the prefrontal cortex; see Pan & Sakagami, 2012 for a review of categorical representations in the prefrontal cortex; see Carol A Seger & Miller, 2010 for a review of the neuroscience of categorical learning). Such task or rule selective activity in LIP (Stoet & Snyder, 2004) might be relayed to LIP from prefrontal regions (Asaad, Rainer, & Miller, 2000) like the dorsolateral prefrontal cortex with which it is structurally connected (Blatt et al., 2004). Through top-down control, the prefrontal cortex might be able to suppress information in more posterior regions when it is irrelevant for the task at hand (Chao & Knight, 1998; Miller & D'Esposito, 2005).

Once an animal has learned to arbitrarily associate a shape cue with saccading to a particular location, the animal almost always looks to the preferred location of a neuron following the presentation of particular shape cues, and looks to the anti-preferred location following the presentation of other shape cues. In the former case, the shape cues are succeeded by increased neural activity due to the orienting behavior itself and the corresponding visual inputs might gradually strengthen over time through small changes of synaptic weights. In the latter case, shape cues are followed by relatively lesser activity and the corresponding visual inputs could get relatively weaker with more experience. Over long periods of time, certain shape cues appear to gain the ability to rapidly and automatically guide attention to a particular spatial location. LIP neurons reflect this by responding to these cues as if a weak visual stimulus was shown in the corresponding empty location. When the association between a visual stimulus

and a response is highly overlearned, LIP thus might become able to support extremely rapid arbitrary visuomotor transformations independent of top-down feedback from regions such as the prefrontal cortex (Swaminathan & Freedman, 2012). Without parietal cortex, the associations could still be remembered, but the associated behavior might both be slower and less automatic as, for example, measured by greater dual-task interference.

The associations are still flexible enough to be sensitive to the situation; LIP shape responses contain information about an associated location, but while this effect is rapid enough to be stimulus-driven, it also appears to be gated. It is only seen in the task in which the shape-action associations were learned, and in which they were behaviorally relevant. These learned shape-induced orienting biases might be suppressed when faced with a task where this information is irrelevant or even counterproductive. This is in accordance with studies that find that the attentional capture of salient visual objects can be modulated or even abolished depending on the current task set (Eimer & Kiss, 2008; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Kiss, Jolicœur, Dell'Acqua, & Eimer, 2008; Hermann J Müller, Geyer, Zehetleitner, & Krummenacher, 2009). Contextual changes in response gain have also been reported in LIP where the responses to salient inputs become greater when they are behaviorally relevant (Balan & Gottlieb, 2006; Gottlieb, Balan, Oristaglio, & Schneider, 2009).

With enough training, any shape might acquire the ability to bias orienting to a particular location. However, our results indicate that not all associations are made equal; some shape-orienting associations appear to be more intuitive than others. Stimulus-driven LIP responses to novel visually presented shapes predict orienting actions in future situations when those shapes are encountered again and become behaviorally relevant. In a nutshell, when a cell responds more to location A than B, and more to shape 1 than 2, then monkeys are more likely to associate shape 1 with orienting to location A, and shape 2 with location B. Our results call into question the assumption that central visual cues are neutral before having been explicitly associated with particular locations. There might not be such a thing as a neutral shape.

Follow-up behavioral work, described in chapter 3, showed that information derived from the shape of even completely novel, randomly generated objects indeed biases the allocation of visual attention and eye movements to particular locations in space. The effects are stimulus-specific and replicable across subjects and tasks. This happens swiftly and automatically without specific learning or training and is not easily overridden by short-term experience. These links

between shape and space can be thought of as initial hypotheses, or first guesses, on where to look and pay attention, and LIP either creates or has access to such information derived from shape. The fact that novel behavioral effects were predicted based on our neurophysiological findings makes it likely that they are generalizable and relevant in several situations.

It is still conceivable that early passive responses to novel shapes predict future orienting because of the specific training the monkeys were given. The learned orienting actions associated with familiar shapes could possibly generalize to novel shapes that share some of their features. This might happen, but we do not think that it can account for our results. If this was the case, we would expect the effects of long-term shape-saccade associations to be apparent in the rapid passive responses to familiar shapes. Instead, it appears that the effects of long-term learning are not present during passive viewing of shapes. We therefore think that the early passive responses to novel shapes reflect an exogenously driven orienting bias that is not experience-dependent in any traditional sense.

Shape responses in LIP can be modified and overridden but not completely overwritten by experience. LIP neurons carry information about the orienting action associated with a shape and which the monkey is going to perform. Literally at the same time the responses to shapes can be distinct even though they were both similarly acted on in the past and will lead to the same orienting behavior in the future. We speculate that persistent response differences to same-meaning shapes would have supported the monkeys' orienting actions at the beginning of training in a similar way as LIP neural responses to novel shapes seemingly bias behavior. The interesting possibility still remains that LIP incorporates a combinatory code of an orienting bias and an object tag (look *there* at *that thing*).

Orienting guided by central cues is often described as endogenous, voluntary, or controlled, as opposed to the exogenous, reflexive, and automatic effects of peripheral cues (Müller & Rabbitt, 1989; Posner, 1980). Some central cues, such as arrows (Ristic & Kingstone, 2006; Tipples, 2002) and eye gaze (Driver et al., 1999; Friesen & Kingstone, 1998), can nonetheless evoke fast reflexive orienting shifts. Eye gaze of a conspecific is also known to affect both a monkey's orienting and the firing rate of a subset of LIP neurons (Shepherd, Klein, Deaner, & Platt, 2009). Extensive training of associating a central shape cue with an orienting response changes the behavior of LIP neurons so that they start to respond to this shape as if it was a visual stimulus presented in the cued spatial location. A former endogenous visual cue

might therefore be said to become exogenous with enough training.

Our current results and several follow-up behavioral experiments described in chapter 3 suggest that even unfamiliar nonsense objects may induce such an orienting bias because of their shape. We speculate that eyes, arrows, and other orienting symbols, through natural and cultural selection, may have acquired their distinctive shape partly because their shape automatically biases — or affords — orienting to particular locations. This bias could then have been further amplified by life-long learning through repeatedly associating such a shape with the appearance of interesting things in the direction to which it points. Our results support the idea that LIP has access to or can carry out the necessary computations for extracting such an orienting bias from shape. This bias could be learned and arbitrary, or directly driven by shape properties that affect the correspondence (Lambert, Roser, Wells, & Heffer, 2005) of an object with the preferred locations of LIP neurons, such as spatial asymmetry, central axis orientation, a salient part of an object, or other factors worth investigating in further studies.

Thinking of LIP shape selectivity as serving the purpose of orienting helps to make sense of the puzzling finding that LIP and its putative human homologue can be relatively tolerant to image transformations like scaling and translation (Janssen et al., 2008; Konen & Kastner, 2008; A. B. Sereno & Maunsell, 1998). Such invariance has most often been thought to be a hallmark of the object- and form-sensitive ventral visual pathway (Booth & Rolls, 1998; Robert Desimone, Albright, Gross, & Bruce, 1984; Gross, 1973; Ito, Tamura, Fujita, & Tanaka, 1995; Logothetis & Sheinberg, 1996; Tanaka, 1996). Visual stimuli can however also show invariance of the orienting bias they evoke, such as when seeing a face tilted 90 degrees evokes orienting shifts to the side to which the person's eyes *would* have been looking had the face been in its canonical upright position (Bayliss & Tipper, 2006; Bayliss, di Pellegrino, & Tipper, 2004), or when words make people orient to the location in which the objects they denote are usually found (Estes, Verges, & Barsalou, 2008). We expect LIP neurons to be relatively invariant to changes in a visual stimulus that preserve not its identity or form but the strength or direction of its orienting bias.

Both eye movements and attention are often probed with simple stimuli such as points or gratings but these are not the things we regularly encounter outside the lab. The rules governing orienting behavior must be tailored to looking at the variably shaped things found in the real world. Our results support the idea that shape information feeds into a specific neural network

that identifies the possible sources of visual information worth exploring further by means of overt and covert orienting.

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CHAPTER THREE

Form-derived directionality of objects: Effects on visual attention and motion perception

Introduction

The visual world is not static; within it, things are moving and we are often moving ourselves — if not our bodies then at least our eyes which constantly scan the visual scene. Processing dynamic input requires efficient extraction of information about the current state of the environment to make predictions about where important things will be in the near future. We should guide our eyes and attention not to an object's previous location, but to where it is likely to be once action can be taken. Fortunately, under normal circumstances, an object does not randomly change location from one moment to the next; its future state depends on its past state. An optimized system would be able to use such information to accurately predict an object's future location or motion path from a single snapshot in time. This could bias both overt and covert visual orienting so that objects can be located, tracked, and sampled even in a dynamic world. Here we test the hypothesis that information derived from an object's shape enables the brain to make such inferences.

Within the visual system, the dorsal pathway's role in visual orienting, tracking, and motion analysis is well-established (Andersen, 1997; Colby & Goldberg, 1999; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Ungerleider & Mishkin, 1982; Van Essen & Gallant, 1994). In addition, some regions of the dorsal stream are responsive to the shape of objects (Grill-Spector & Malach, 2004; Janssen, Srivastava, Ombelet, & Orban, 2008; Konen & Kastner, 2008; Lehky & Sereno, 2007; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Oliver & Thompson-Schill, 2003; Red, Patel, & Sereno, 2012; Sakata et al., 1998; Sakata, Taira, Murata, & Mine, 1995; A. B. Sereno & Amador, 2006; A. B. Sereno & Maunsell, 1998; M. E. Sereno, Trinath, Augath, & Logothetis, 2002; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). The fact that shape selectivity exists in cortical areas beyond the ventral visual stream (Desimone, Albright, Gross, & Bruce, 1984; Gross, Rocha-Miranda, & Bender, 1972; Logothetis & Sheinberg, 1996; Tanaka, Saito, Fukada, & Moriya, 1991) argues against regional specialization for particular stimulus attributes, emphasizing the need to consider function and goal in relation to object properties. Shape information might be integrated with various other cues and tailored to a particular process or task. Indeed, the shape of an object influences processes thought to depend on the dorsal visual stream, such as visual orienting and estimation of motion, in addition to object recognition and categorization, which are classically linked with the ventral visual stream.

For example, the oculomotor system seems able to take into account the global shape of an object during saccade planning (He & Kowler, 1991). This kind of visual orienting does not merely depend on low-level averaging of visual elements but has access to a higher level representation of the object's shape (Melcher & Kowler, 1999). This shape information may be partially or wholly independent from the representation used for perception (Vishwanath, Kowler, & Feldman, 2000). The shape of an object guides overt and covert attention within the object itself and can, in special cases, push attention away (Driver et al., 1999; Fischer, Castel, Dodd, & Pratt, 2003; Friesen & Kingstone, 1998; Hommel, Pratt, Colzato, & Godijn, 2001; Kuhn & Kingstone, 2009; Tipples, 2002, 2008). An arrow is a prime example. Despite initial thoughts to the contrary (Jonides, 1981), arrows automatically bias orienting (Hommel et al., 2001; Kuhn & Kingstone, 2009; Tipples, 2002, 2008). This may be partially due to repeated association of this particular shape and its referent; something often appears in the direction to which an arrow is pointing. Here, we argue that this association is not arbitrary; initially, the symbol might have been selected because its shape already had an inherent directionality that automatically evoked an orienting bias. This bias might again be derived from the fact that the structure of a real arrow facilitates a stable flight path in a single direction. In general, the shape of objects constrains their movements. It would therefore be beneficial for the visual system to use shape information to predict an object's probable motion path and to use such predictions for overt and covert visual orienting.

Shape or form cues are integrated into motion calculations, (see Kourtzi, Krekelberg, & van Wezel, 2008, for a review). For example, the oriented trace or streak left by a fast-moving object determines its perceived axis of motion (Burr & Ross, 2002; Geisler, 1999). Dynamic Glass patterns, which contain no coherent motion, can also lead to the perception of movement and affect the tuning of motion selective neurons (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Krekelberg, Vatakis, & Kourtzi, 2005; Ross, Badcock, & Hayes, 2000). Likewise, still photographs depicting objects in motion evoke greater activation in motion selective cortical regions than do photographs of stationary objects (Kourtzi & Kanwisher, 2000; Senior et al., 2000). An object's remembered location is also shifted along its implied path of motion (Freyd & Finke, 1984). This shift is lost when motion selective cortical regions are temporarily deactivated (Senior, Ward, & David, 2002). With some exceptions (e.g. Caplovitz & Tse, 2007; Tse & Logothetis, 2002), most studies on the effects of form or shape cues on motion

involved simple non-object-like stimuli (e.g. motion streaks, Glass patterns), or recognizable animate or inanimate objects or scenes depicting familiar events or actions.

The studies described in this paper were stimulated by the idea that shape information existing in dorsal stream regions is tailored to and supports the function of these areas in spatial perception and action guidance (Goodale & Milner, 1992; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). We explore the role of shape information in visual orienting and motion calculation which have well-known neural substrates in the dorsal stream. In experiments 1 and 2, we establish that people consistently deem novel shapes to "point" in particular directions. We then look at the effects of this shape-derived directionality on visual orienting (experiments 3, 4, and 7) and motion perception (experiments 5, 6, and 7).

Our work shows that objects have intrinsic directionality derived from their shape. This shape information is swiftly and automatically incorporated into the allocation of overt and covert visual orienting and the detection of motion, processes which are inherently directional. While covert attention might be split under some unusual circumstances (Awh & Pashler, 2000; Hahn & Kramer, 1998; Kramer & Hahn, 1995), our eyes only move in one direction at a time. Likewise, a single object only moves in one direction at any given time point. Attention is automatically pushed away from the object in a direction that depends on the object's shape. This in turn is incorporated into the calculation of the object's probable path of movement; detection of an object's direction of motion is facilitated if it is congruent with the inherent shape-derived directionality of the object and hindered if shape directionality and motion directionality oppose each other. Importantly, such form-dependent directional biases are not limited to well-known or over-learned objects or tasks. Instead, they are seen for meaningless shapes, with which people have no prior experience, in a variety of settings and regardless of whether people have any intent or reason to use this directional information. This suggests that shape-related directional biases are ever present and are given weight in predictions or simulations of the upcoming state of the environment or, more specifically, where important objects will likely be located in the immediate future.

Experiments: Methodological Overview

A total of 114 people participated in one of seven experiments. Each person took part only once. They reported normal or corrected to normal vision and were paid for their participation. All participants gave their written consent. The experimental protocol was approved by Brown University's Institutional Review Board.

The experiments were controlled by a computer console running on the QNX real-time operating system (QSSL; QNX Software Systems). It communicated with a Windows XP PC through a direct high-speed Ethernet connection. This computer ran custom-made software based on OpenGL for graphics display. In experiments 1-3, stimuli were shown on a standard 20" cathode ray tube monitor (width: 41 cm; height: 30 cm) with 1024 x 768 resolution. In experiments 5-7, they were shown on a high speed 23" widescreen LCD monitor (width: 51 cm; height: 28 cm) with 1920 x 1080 resolution. In experiment 4, half of the participants were run using the former setup, and half the latter. The monitors' vertical refresh rate was 100 Hz for all experiments. The displays were placed at a distance of 57 cm in front of the subjects.

Participants were seated in a dark, quiet room in front of a computer screen. A black curtain was draped around them and the computer screen. Participants' heads were held still by a chin rest. In experiments 3, 4, and 7, people's eye movements were monitored with an EyeLink 1000 eye tracker (SR Research). A high-speed camera and an infrared light source were desk-mounted under the computer monitor. Eye gaze was monocularly recorded at 1000 Hz. The analog signal was sampled and digitized at 200 Hz. The eye tracker was calibrated by asking participants to saccade to and fixate several small targets that appeared in random locations on the screen. Eye tracking was not performed in experiments 1, 2, 5, and 6.

An alpha level of 0.05 is assumed for all statistical analysis of the data. Statistical tests are two-sided. Results are Greenhouse-Geisser corrected for deviations from sphericity when Mauchly's test of sphericity is significant. Effect sizes are estimated using Pearson's r, Cohen's d (mean difference / standard deviation of difference) and partial eta squared (η_p^2). Error bars represent 95% confidence intervals for within-subject comparisons and are calculated using Cousineau's method (2005) with the correction described by Morey (2008).

Experiment 1: Directionality Assessment

The aim of experiment 1 was to assess the extent to which people agree on the directionality of objects based on their shape alone. We did not want to constrain the interpretation of our results with our preconceptions about what might make a shape directional. We therefore constructed a variety of random shapes with which people had no previous experience and empirically determined their directionality. We asked people to judge where each of the novel shapes pointed or directed them and determined if people's judgments were more similar than would be expected by chance. If judgments of a majority of the shapes deviate from circular uniformity, we would conclude that directionality is a general property of a wide variety of shapes.

Method

Participants. 16 people (9 women) participated in this experiment. Their ages ranged from 18 to 36 (M=25).

Stimuli. 80 novel shapes were generated by superimposing two filled polygons. Each polygon was made by fitting a spline to randomly generated coordinates (8 for simple or 16 for complex shapes) on a 2D plane. The algorithm was based on the General Polygon Clipper library (v. 2.32) which is freely available for non-commercial use (Murta, 2000; see also Vatti, 1992). Shapes were scaled to an equal area. Their diameter was approximately 4°. Of the 80 shapes, 20 were made symmetrical by reflecting one side around the y-axis. The contours of the shapes were densely sampled and translated so that the means of their contour coordinates would coincide. Each shape was randomly rotated around this pivot and kept this rotation throughout the experiment and for all participants. The same method was used to make additional shapes for a short practice session. All shapes were shown as white, filled silhouettes. The shapes can be seen in figure 3.1.

Design. Each person completed 360 trials, out of which 40 were control trials and 320 were experimental trials (80 shapes x 4 repetitions). The trials were spread across five blocks and were shown in a randomized order with the constraint that 8 control trials were shown in each block.

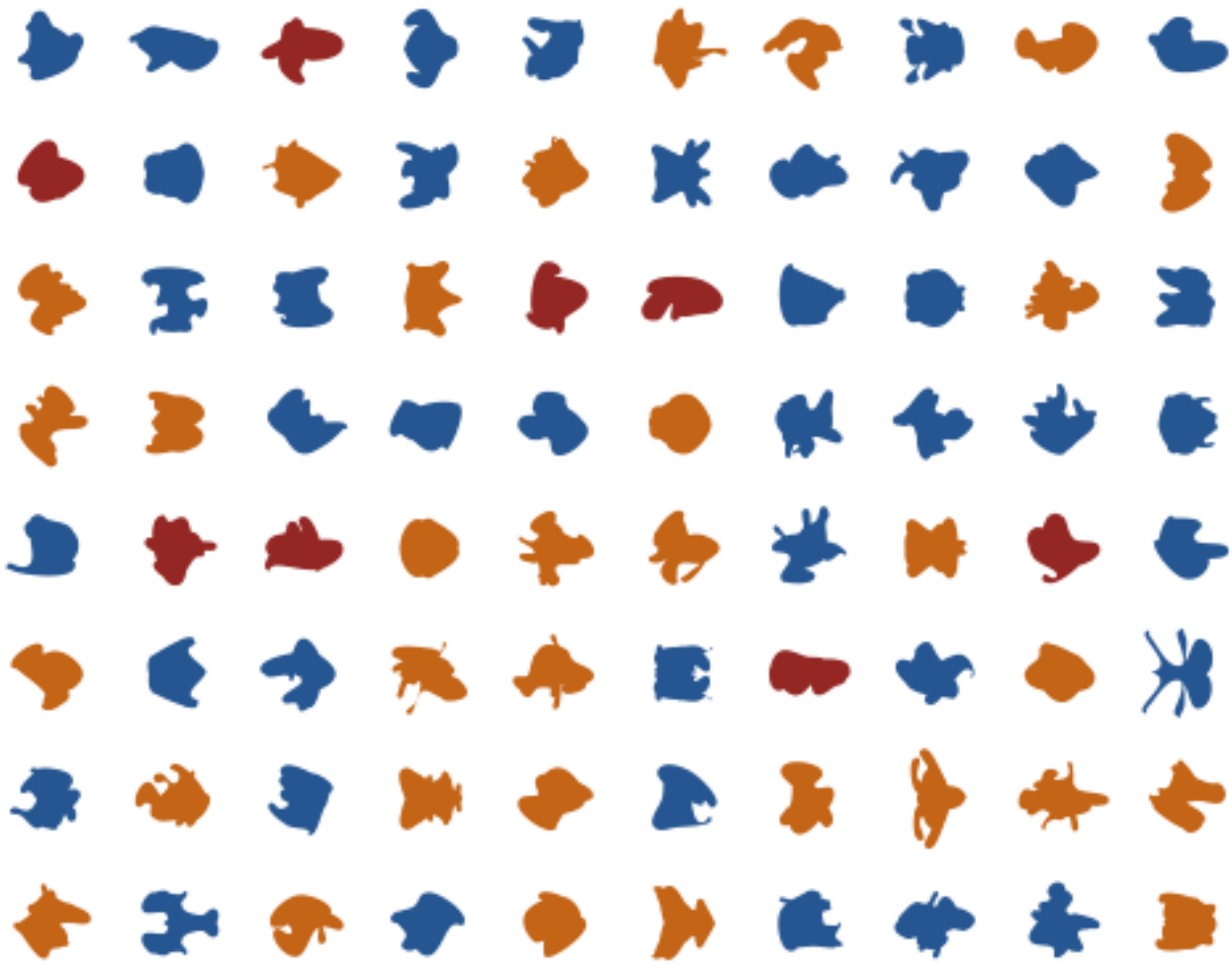

Figure 3.1. All novel shapes. Shapes are shown pointing to the right, as judged by people in experiment 2. All novel shapes were used in experiments 1 and 2. Red and orange shapes were used in experiments 3, 5, 6, and 7. Red shapes were used in experiment 4.

Procedure. People were instructed to look to the center of the screen at the beginning of each trial. A single central shape and a surrounding gray circle (diameter 26°) were presented on a black background. The shape was on for 100 ms but the circle stayed visible throughout the trial. The task is depicted in figure 3.2.

People used a computer mouse to drag a gray line in the direction to which they thought the shape pointed or directed them; longer lines indicated stronger confidence. The line was drawn in real time from the screen center to the current position of a gray circular cursor (diameter 0.4°) and could be drawn as far as to the surrounding circle. Participants clicked the

left mouse button to indicate their response. They were encouraged to not think much about their responses but instead go with their intuition.

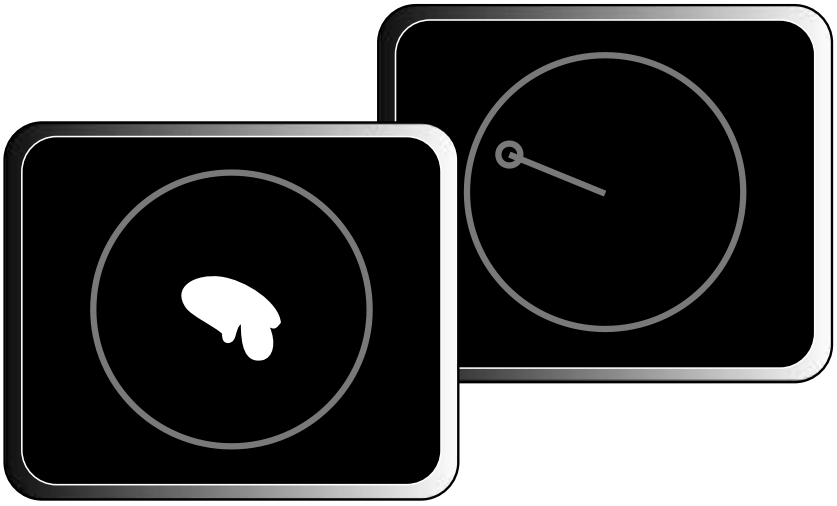

Figure 3.2. Task in experiment 1. People judged the directionality of novel shapes by dragging a line in the direction to which they thought the shapes pointed or directed them.

In a minority of trials, no shape was shown and participants instead dragged a line to the position of a small disk. All participants performed well on these control trials, ensuring us that they paid attention to the task at hand and could position the line appropriately. Before beginning the experiment, people completed a short practice block.

Results

Each of the 16 participants judged the direction of each shape four times, giving a total of 64 data points for each of the 80 random shapes. All shapes with their directional judgments are shown in figure 3.3.

We tested for circular uniformity of the directional judgments of each shape. Visual inspection of the click endpoints indicated that some of the shapes were unidirectional, some were bidirectional, and yet others were multidirectional. We therefore performed two different statistical tests on each shape: A Raleigh test and Rao's spacing test. The Raleigh test assumes that the samples are drawn from a von Mises distribution (analogous to the normal distribution for non-circular data) and is useful for detecting deviations from uniformity when a shape has one main direction (Berens, 2009). Rao's spacing test can detect deviations from a uniform

distribution for shapes that are neither unidirectional nor axially bidirectional (Berens, 2009).

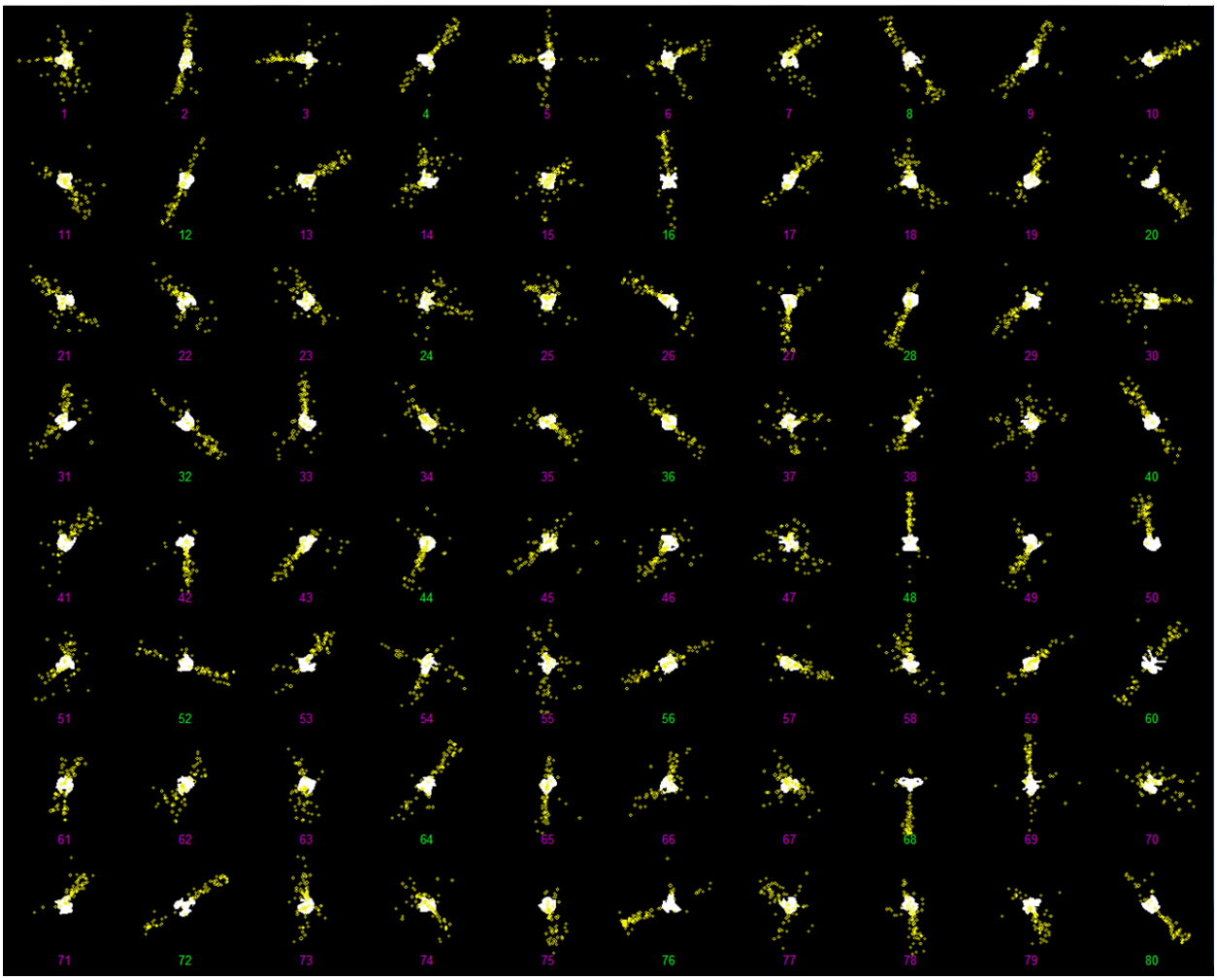

Figure 3.3. All shapes and directional judgments. 80 novel shapes are shown with the endpoints (yellow circles) of all "drag-and-clicks" used for directional judgments in experiment 1. Asymmetrical shapes are marked with a magenta number, and symmetrical shapes are marked with a green number.

A participant's decision criterion for assigning directionality could evolve over the course of the experiment. For each shape, we therefore tested for significant deviations from circular uniformity using only the first directional judgment of each participant. Instead of using all 64 judgments, we therefore only used 16 data points per shape, effectively lowering our statistical power.

Table 3.1. Statistics for tests of circular uniformity: Shapes 1-40. For each shape, the first directional assessment of every participant was used, giving a total of 16 data points for each test. A star symbol (*) is used to indicate that the directional assessments of a shape significantly deviate from circular uniformity. The approximate p-values for Rao's spacing test are, more specifically, the smallest commonly used alpha levels at which the test would be significant. The statistics are calculated using the Circular Statistics Toolbox for MATLAB (Berens, 2009). Shape numbers correspond to those in figure 3.3.

Shape number	Raleigh sig.	Rao sig.	Raleigh test p	Rao test approx. p	Raleigh test z	Rao test U
1		*	0.194	0.001	1.647	205.897
2		*	0.821	0.001	0.203	232.472
3	*	*	0.001	0.001	6.211	209.615
4		*	0.153	0.001	1.883	237.606
5	*	*	0.032	0.010	3.359	197.272
6	*	*	0.001	0.010	6.305	193.523
7	*	*	0.025	0.010	3.579	190.742
8		*	0.531	0.001	0.647	245.497
9		*	0.253	0.001	1.388	245.916
10	*	*	0.009	0.001	4.533	233.295
11	*	*	0.000	0.001	8.352	208.074
12		*	0.127	0.001	2.058	251.404
13		*	0.155	0.001	1.870	216.825
14	*	*	0.006	0.001	4.817	205.763
15			0.078	0.100	2.528	162.636
16	*	*	0.014	0.001	4.099	248.612
17	*	*	0.020	0.001	3.813	254.921
18		*	0.242	0.010	1.432	190.070
19	*	*	0.000	0.001	8.461	255.906
20	*	*	0.035	0.001	3.285	216.481
21		*	0.185	0.001	1.697	205.582
22			0.375	0.500	0.997	120.003
23			0.112	0.500	2.187	140.752
24	*	*	0.013	0.010	4.171	181.955
25			0.085	0.500	2.451	154.749
26	*	*	0.012	0.001	4.246	257.106
27	*	*	0.002	0.001	5.762	244.474
28	*	*	0.000	0.001	8.822	250.487
29	*	*	0.001	0.001	6.843	244.602
30	*	*	0.031	0.001	3.396	201.711
31	*	*	0.000	0.001	7.255	202.812
32		*	0.083	0.001	2.469	242.573
33	*	*	0.000	0.001	12.307	300.685
34		*	0.845	0.050	0.173	173.079
35	*	*	0.007	0.001	4.698	234.866
36	*	*	0.002	0.001	5.729	245.202
37			0.080	0.500	2.502	146.174
38		*	0.680	0.001	0.396	208.741
39		*	0.589	0.050	0.542	174.603
40		*	0.116	0.001	2.153	267.530

Table 3.2. Statistics for tests of circular uniformity: Shapes 41-80.

Shape number	Raleigh sig.	Rao sig.	Raleigh test p	Rao test approx. p	Raleigh test z	Rao test U
41	*	*	0.000	0.001	8.986	232.536
42	*	*	0.000	0.001	11.904	277.456
43		*	0.106	0.001	2.236	213.769
44	*	*	0.005	0.001	5.093	213.188
45			0.642	0.500	0.454	147.183
46	*	*	0.014	0.010	4.097	195.864
47		*	0.161	0.050	1.831	173.809
48	*	*	0.000	0.001	9.770	259.228
49	*	*	0.000	0.001	7.538	218.907
50	*	*	0.000	0.001	15.433	289.695
51		*	0.111	0.001	2.195	203.287
52		*	0.918	0.001	0.088	237.879
53	*	*	0.001	0.001	6.406	252.947
54		*	0.173	0.050	1.763	179.642
55		*	0.202	0.010	1.608	191.221
56		*	0.249	0.001	1.402	239.678
57		*	0.204	0.001	1.600	219.477
58	*	*	0.023	0.001	3.664	206.461
59		*	0.862	0.050	0.153	177.881
60		*	0.437	0.001	0.843	212.720
61		*	0.080	0.001	2.510	226.996
62		*	0.217	0.010	1.541	188.522
63	*	*	0.008	0.001	4.650	240.977
64		*	0.276	0.001	1.302	250.957
65	*	*	0.017	0.001	3.959	293.582
66		*	0.922	0.010	0.083	188.113
67			0.542	0.500	0.626	120.362
68	*	*	0.000	0.001	9.786	259.450
69	*	*	0.000	0.001	11.174	263.524
70			0.393	0.500	0.951	118.182
71	*	*	0.000	0.001	15.302	289.076
72	*	*	0.011	0.001	4.362	268.886
73	*	*	0.001	0.001	6.799	255.894
74			0.115	0.100	2.154	163.870
75	*	*	0.001	0.001	6.521	219.271
76		*	0.165	0.001	1.807	243.226
77	*	*	0.037	0.001	3.232	215.638
78	*	*	0.000	0.001	7.363	224.046
79	*	*	0.000	0.001	10.414	228.688
80	*	*	0.007	0.001	4.697	274.084

Despite this rather conservative way of analyzing the data, the Raleigh test rejected the null hypothesis that the drag-and-clicks were uniformly distributed for 42 out of 80 shapes. Rao's spacing test was significant for nearly all of the shapes, or 71 out of 80. Test statistics can be found in tables 3.1 and 3.2. We therefore conclude that novel, random shapes in general are directional. A majority of completely novel shapes has an inherent directionality, be it unidirectional, bidirectional, or multidirectional. Figure 3.4 shows all directional judgments from experiment 1, regardless of shape.

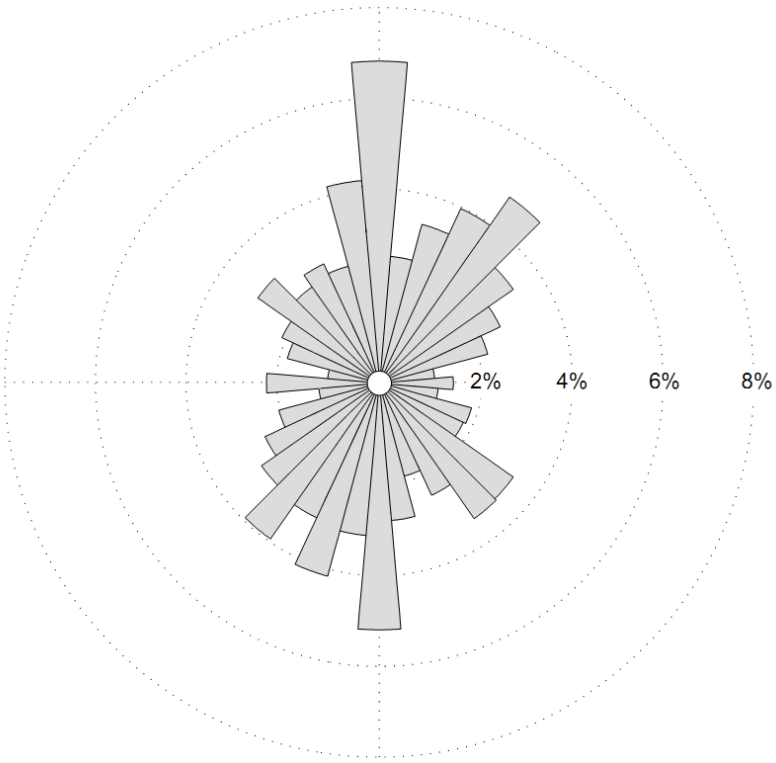

Figure 3.4. All directional judgments. This rose plot, or angle histogram, shows people's drag-and-clicks used for directional judgments in experiment 1. All drag-and-clicks are included, regardless of which shape stimuli were shown. The length of each bin corresponds to the percentage of drag-and-clicks that fell within the corresponding directions.

Experiment 2: Forced Choice of Directionality

Experiment 1 showed that directional judgments are non-uniform for a majority of randomly shaped novel objects. However, judgments also appeared to be influenced by factors that were independent of, or interacted with, the shape of these objects (figure 3.4). Even if the rotation of the shapes was randomly determined, people in general tended to favor an upward and to some

lesser extent a downward direction. People might have been following a heuristic akin to “when in doubt, an object is aligned to the axis of gravity”. The benefits of transient visual attention have also been documented to be greater in the upper than the lower visual hemifield (Kristjánsson & Sigurdardottir, 2008), and this could be a contributing factor. It is also possible that the response mode introduced some bias. To minimize such biases, experiment 2 involved a more constrained judgment about the directionality of the same shapes with a new set of subjects.

The main purpose of experiment 2 was to get unbiased measurements of each shape’s perceived directionality so that these measures could be used as predictors of behavior in experiments 3-7. We also wanted to know whether we could assume that directionality was independent of the time of probing. Neurons within dorsal stream regions important for the allocation of attention and eye movements respond selectively to shapes, but these shape responses can change very rapidly over the course of a few hundred milliseconds (see chapter 2). We therefore thought it possible that the perceived direction of a shape could change very rapidly as well and thus we included two different stimulus onset asynchronies in this experiment.

Method

Participants. 14 new participants (9 women) completed experiment 2. They were between 18 and 31 years of age (M=23).

Stimuli. The 80 shapes used in experiment 1 were also used in experiment 2. We found the median axis of the directional estimates gathered for each shape in experiment 1. Note that the axis itself has an orientation but not a direction; for example, directional judgments to the left and right would similarly favor a horizontal axis, and up and down directional judgments would count toward a vertical axis. All shapes were then rotated so that this main axis fell on the horizontal meridian. Clockwise or anti-clockwise rotation was chosen for each shape, whichever one led to a rotation of fewer degrees from the shape’s orientation in experiment 1. Each shape was shown in this alignment (original) or reflected across the vertical meridian (mirrored).

Design. Each person completed 320 trials spread across five experimental blocks in a random order. The 80 shapes were shown four times each, twice in the original alignment and twice mirrored to ensure that any possible left-right biases would not systematically influence

people's directional judgments. Each shape was followed by two peripheral disks with a 150 ms or 300 ms stimulus onset asynchrony (80 shapes x 2 alignments x 2 SOAs).

Procedure. The behavioral task from experiment 2 can be seen in figure 3.5. People were asked to look to the center of the screen at the start of each trial. A white shape (diameter approximately 4°) appeared on a black background in the center of the screen followed by the onset of two gray disks (diameter 2°), one on the left and the other on the right side of the screen (8° eccentricity). The shape and the disks stayed on the screen until the person responded.

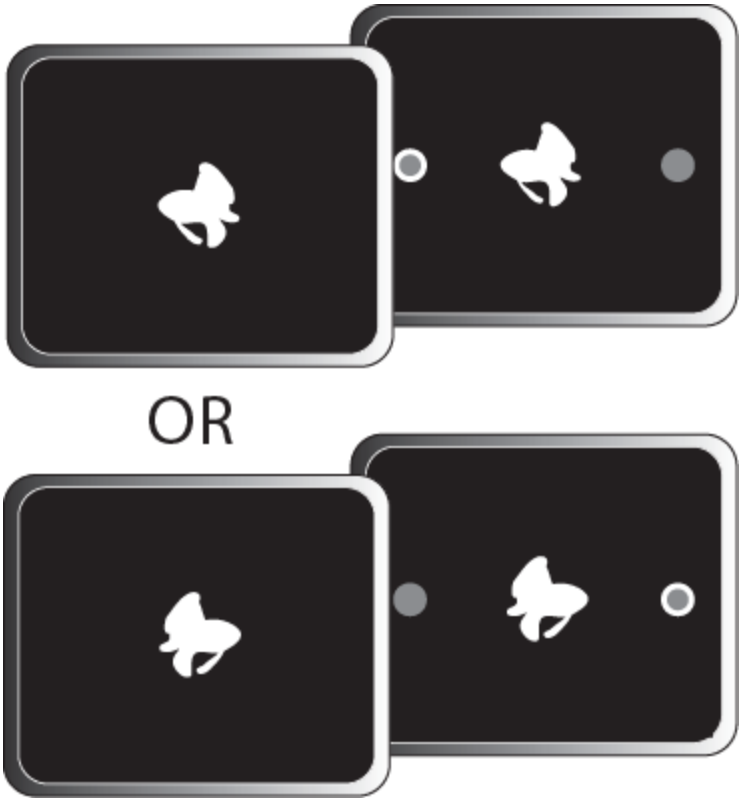

Figure 3.5. Task in experiments 2 and 3. In experiment 2, a central shape was shown, followed by the appearance of two peripheral disks. Participants indicated whether the shape pointed or directed them to the left or right disk by pressing one of two response buttons. These judgments were used as indicators of each shape's directionality. In experiment 3, a shape was followed by the display of only a single disk which could appear with equal likelihood in a direction congruent or incongruent with the shape's inherent directionality. Subjects indicated which side of the screen the disk appeared on by pressing the appropriate button. An example congruent disk is marked here with a white circle; no white circles were shown in the actual experiments.

Participants held a button box with both hands. They were instructed to push the left button if they thought a shape pointed or directed them to the left dot, and push the right button if they thought a shape pointed or directed them to the right dot. They were told to respond as soon as the dots appeared and were informed that there were no correct or incorrect responses for any of the shapes. Each person completed a short practice session with separate shapes.

Results

For each stimulus onset asynchrony (150 ms and 300 ms), we calculated a measure of a shape's directionality. We did so by determining whether a shape and its mirror image were reported to have opposite directionality. If they did, the participant was said to have determined that a shape had a particular directionality which we arbitrarily call positive and negative (positive: original shape pointed left, mirror image right; negative: vice versa). We then counted the number of participants that indicated that a particular shape had a positive directionality, subtracted the number of participants that reported that the shape had a negative directionality, and divided the difference by the total number of participants. This measure of directionality can theoretically range from -1 (all participants indicate a negative directionality) to 1 (all participants indicate a positive directionality).

As can be seen in figure 3.6, there is a high correlation between the directionality of the shapes at the two stimulus onset asynchronies ($r(78)=0.91$, $p=3.9\times10^{-32}$) and the regression line passes through the origin (y-intercept is not statistically different from 0, $p=0.475$). Therefore, a shape's directionality appears to be unaffected by the time of probing. The high correlation between the two measures indicates that they are capturing the same construct (i.e. directionality) with some added noise.

We therefore combined the measures by taking their average. The measure's sign was used in all following experiments as a binary statistic indicating each shape's directionality, i.e. was a shape deemed to be leftward or rightward in its original position? The measure's absolute value was used in a cross-experiments analysis as an indicator of directionality strength or consensus (see Individual Item Analysis).

A two-factor ANOVA with directionality strength as a dependent measure did not reveal any significant effects of either the complexity of the shapes (whether their polygons were made by fitting a spline to 8 or 16 coordinates) or whether they were symmetric or asymmetric (main effect of complexity: $F(1,76) = 2.860$, $p = 0.095$; main effect of symmetry: $F(1,76) = 1.730$, $p = 0.192$; interaction: $F(1,76) = 0.022$, $p = 0.882$).

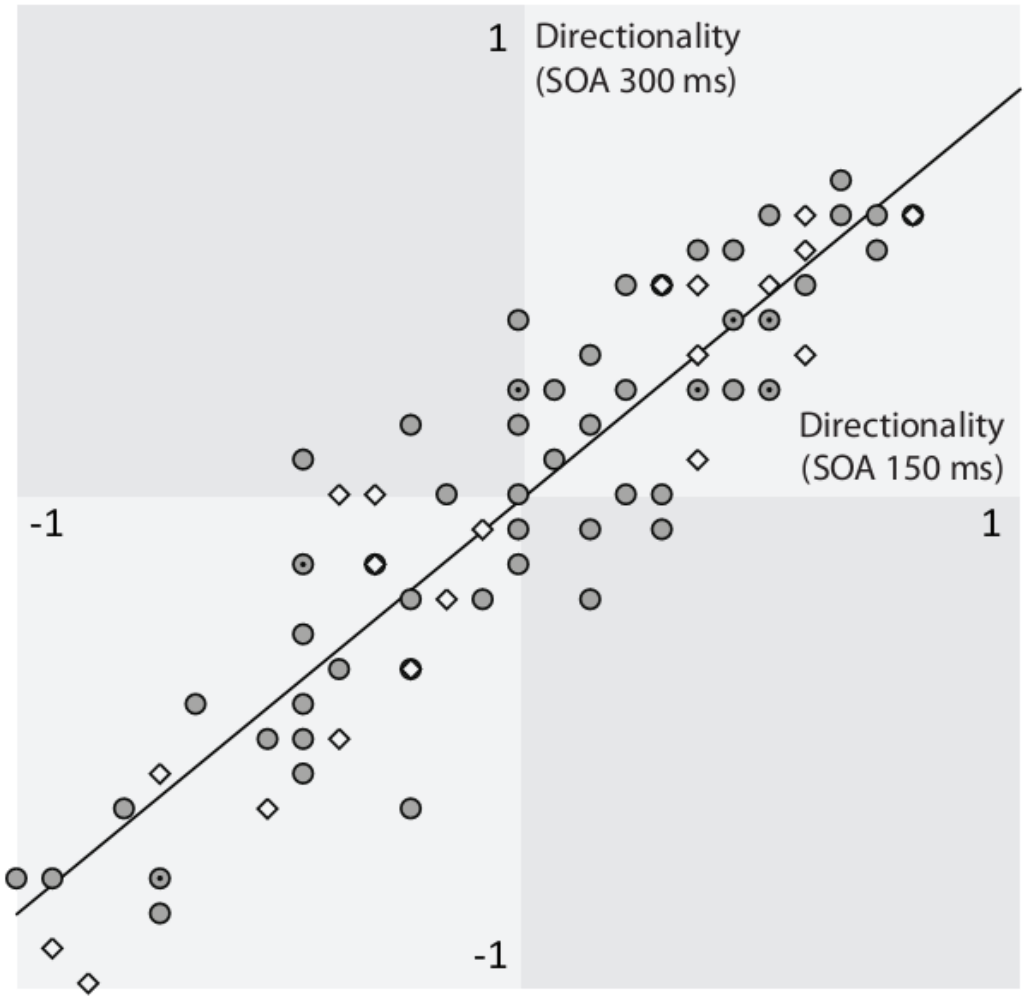

Figure 3.6. Directionality of novel shapes. Each novel shape's directionality is indicated by a marker. Symmetrical shapes are marked with a light gray diamond, and asymmetrical shapes with a dark gray circle. A diamond embedded in a circle is a marker for two different shapes, one symmetrical and the other asymmetrical. A circle marked with a dot represents two asymmetrical shapes. Directionality can theoretically range from -1 (everyone judges a shape to have negative directionality) to 1 (everyone judges a shape to have positive directionality). Directionality judgments were highly similar at two stimulus onset asynchronies. For details, see Experiment 2: Forced Choice of Directionality.

Experiment 3: Shape-Induced Covert Visual Orienting of Attention

Our claim is that the capability of biasing orienting is a general property of shape, even without explicit training or learning, instead of being limited to a select few over-learned objects. In experiment 3, we therefore used several novel shapes and asked if they automatically pushed visual attention in a particular direction. We would reach this conclusion if people were faster at detecting visual targets when novel shapes pointed to their location even though targets were no more likely to appear there than they were to appear in the opposite direction. We additionally wanted to see whether these effects were time-sensitive. We expected the shape of the objects to rapidly and automatically lead to the formation of an initial hypothesis of where to pay attention, soon to be rejected because relying on the shapes' directionality was maladaptive for performance in the task. We therefore expected a rapid waxing and waning of the effects of shape-derived directionality on the allocation of spatial attention akin to the time course of transient visual attention (see e.g. Nakayama & Mackeben, 1989).

Method

Participants. Subjects were 20 people (12 women), ages 18 to 28 (M=21).

Stimuli. 40 out of 80 shapes used in experiment 2 were used as stimuli in experiment 3. The shapes with the strongest directionality, as determined by responses in experiment 2, were used with the constraints that the proportions of shape types (symmetric or asymmetric, generated from 8 or 16 coordinate polygons) were the same as in the original shape set. Stimuli were displayed as described for experiment 2.

Design. Each person completed 960 trials in a random order. The trials were spread over 10 blocks and were completed in a single day. Each shape was shown equally often in its original alignment and mirrored (see experiment 2). A disk target followed the shape onset with a stimulus onset asynchrony (SOA) of 0 ms, 50 ms, 100 ms, 150 ms, 300 ms, or 500 ms. The design was fully crossed (40 shapes x 2 polarities x 2 disk locations x 6 SOAs) so the shapes predicted neither where nor when a target would appear.

Procedure. Eye position was monitored with an EyeLink 1000 eye tracker (SR Research). Participants had to maintain fixation within 0.65 degrees of the center throughout

each experimental trial, otherwise it would abort. Participants held a response button box with both hands. A shape was displayed in the center. A single gray disk target (diameter 2°) appeared with a variable time delay on the horizontal meridian, either on the left or the right side of the screen at an eccentricity of 8°. Shapes did not predict either where or when a target would appear. The task is depicted in figure 3.5.

People were instructed to press the left button if this target appeared on the left and press the right button if it appeared on the right. They were asked to do this as fast as they could while keeping their responses nearly 100% correct. Before data collection began, participants completed a short practice session with a circular shape.

It should be noted that data from a secondary task were collected from participants in experiment 3. This secondary task was a replication of experiment 2 except that the stimulus onset asynchrony (SOA) was fixed at 150 ms. Before their main session (procedure described above), participants judged the directionality of those 40 out of the original 80 shapes that were not used as stimuli in experiment 3. After their main session, participants judged the directionality of the 40 remaining shapes that were used as stimuli in experiment 3. The data from the secondary task were not used since responses in experiment 3 could be sufficiently predicted based on data collected from an independent group of people who participated in experiment 2, as described in the Results below.

Results

Overall accuracy ranged from 92-100%. Accuracy was slightly, but significantly, greater on congruent (M=98.2%) than incongruent trials (M=97.7%, paired samples t-test, $t(19) = 2.301$, $p=0.033$, $d=0.51$). A trial was considered congruent if a central shape pointed in the direction of a peripheral target, as determined by an independent sample of participants in experiment 2, and incongruent if the shape pointed in the opposite direction. We looked at effects on response times for correct trials only.

13 people completed all 960 trials with full eye tracking. Seven people either did not complete all trials, or completed all trials but we were unable to track their eyes for the whole duration of the experiment. The results for these two groups were qualitatively similar, and similar conclusions would be drawn from statistical analysis on their data. We therefore included data from all subjects in an ANOVA with response time as a dependent measure and two

repeated factors, congruency and stimulus onset asynchrony (SOA, the time between the onset of the shape and the target). Response time was considered to be the time between target onset and manual response.

People were significantly faster when the shapes' directionality was congruent with the target location (figure 3.7, $F(1,19)=22.159$, $p=1.5x10^{-4}$, $\eta_p^2=0.54$). The mean response time also decreased as more time passed between the onset of the shape and the target ($F(1.76,33.40) = 75.91$, $p=4.5x10^{-13}$, $\eta_p^2=0.80$). The interaction between congruency and stimulus onset asynchrony was only marginally significant ($F(5,95)=1.967$, $p=0.090$). Joint tests of the effects of congruency within each level of stimulus onset asynchrony showed that 50 ms was the earliest SOA at which congruency had a significant effect on response time ($F(1, 95)=21.32$, $p=1.5x10^{-5,}$ Bonferroni corrected threshold for significance: 0.008, d=0.99).

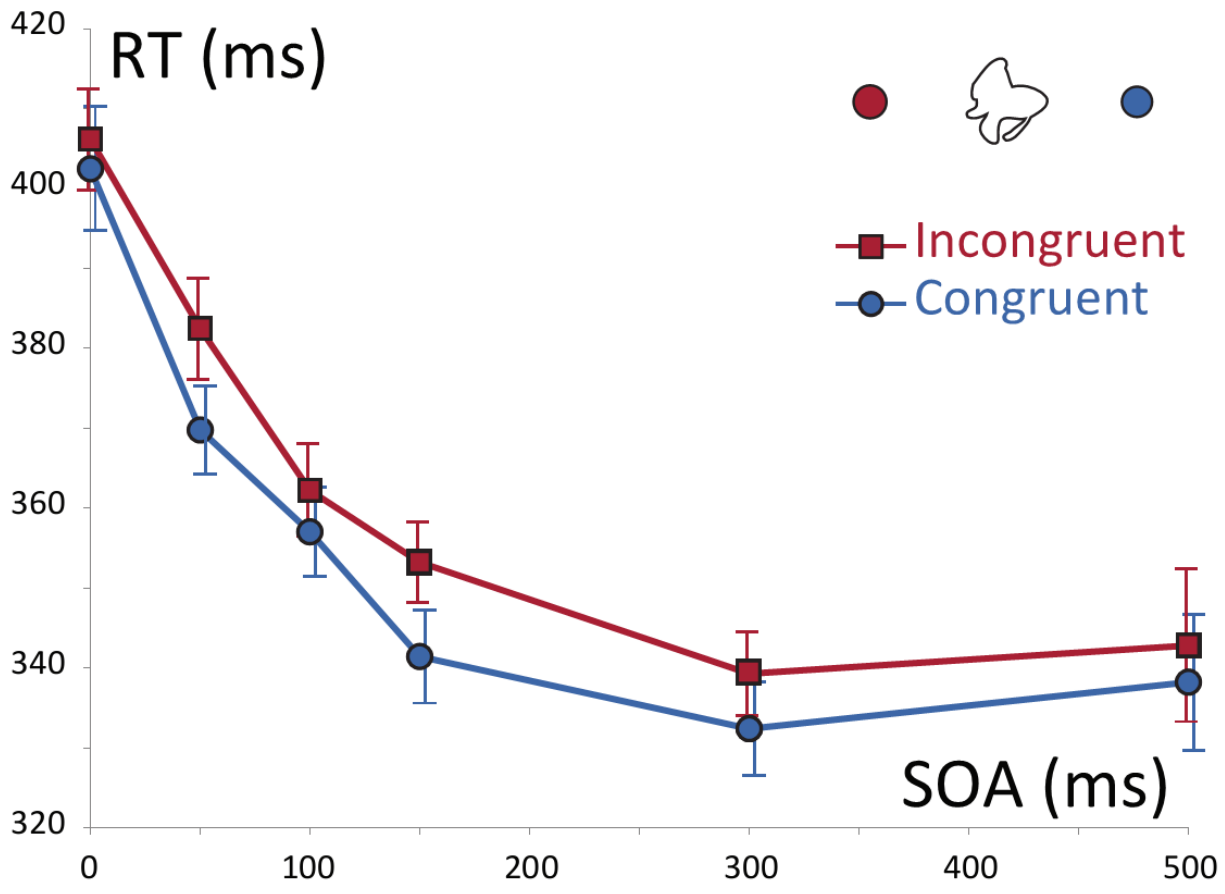

Figure 3.7. Shape-induced orienting of attention. Mean response times (RT) from experiment 3 are shown as a function of stimulus onset asynchrony (SOA) and whether the location of a target was congruent or incongruent with the inherent directionality of a non-predictive central shape cue.

All participants in experiment 3 were right handed. It is conceivable that congruency effects were mainly driven by trials when the target was on the right and the participants thus responded with their dominant hand. Using only correct trials, we therefore performed another ANOVA with response time as a dependent measure and three repeated factors: Congruency, stimulus onset asynchrony (SOA), and target position (on the left or right). The main effects of congruency ($F(1,19)=21.25$, $p=1.9\times10^{-4}$, $\eta_p^2=0.53$), SOA ($F(1.71,32.44)=76.60$, $p=4.0\times10^{-13}$, $\eta_p^2=0.80$), and target position ($F(1,19)=5.26$, $p=0.033$, $\eta_p^2=0.22$) were all significant, as was the interaction between SOA and target location ($F(3.10,58.89)=6.44$, $p=3.4\times10^{-5}$, $\eta_p^2=0.25$). People were faster on congruent trials, they got faster as SOA increased, they were faster for left than for right targets, and this difference for left and right targets decreased with longer SOAs. There was, however, no significant interaction between congruency and target location ($F(1,19)=0.04$, $p=0.85$), nor a significant three-way interaction of congruency, SOA, and target location ($F(5,95)=1.03$, $p=0.41$). The congruency effect does therefore not appear to depend on the target's position or the hand used to report it.

Interestingly, there was enough variability explained by target location that when it was included as a factor in the ANOVA, a significant interaction between congruency and SOA was revealed ($F(5,95)=2.41$, $p=0.042$, $\eta_p^2=0.11$). The dependency of the congruency effect on SOA was close to but not exactly as expected. We had hypothesized that the congruency effects would have a sharp monotonous increase followed by a decrease. Instead, the congruency effects appeared to peak twice, once at the 50 ms SOA and again at the 150 ms SOA. Although surprising, two peaks at approximately those same time points have been reported before for transient visual attention (Nakayama & Mackeben, 1989, see e.g. their fig. 7). We will leave it to future studies to find out whether there might be two processes underlying the effects we see here.

To summarize, people in general are both faster and more accurate at detecting a single target if its location is congruent with the directionality of a non-predictive central shape cue. The congruency effects vary with stimulus onset asynchrony, and are apparent very early on, as early as 50 ms after visual onset of a shape.

Experiment 4: Overcoming Shape-Induced Biases

Experiment 3 showed that the shape of an object rapidly and automatically pushes covert attention in a particular direction. How easily can this bias be overcome? Experiment 3 was deliberately set up to have no cue-target contingencies, making the shape useless with regard to the subjects' detection task. In experiment 4, all shapes provided accurate information about the location of an upcoming target. However, some cue-target contingencies were in accordance with the shape's directionality while others conflicted with it. Would experience with these cue-target contingencies make people overcome their initial shape-induced biases?

We designed a task where a target always appeared in the location to which some shapes pointed, while for other shapes it always appeared in the location that they pointed away from. If people are consistently faster at finding the target in the former case than in the latter, even though all shape cues are informative, we would conclude that a shape's directionality influences behavior not only in a situation when there is nothing else to go on, but also comes into play even when other, more accurate information is available.

Method

Participants. 16 people (6 women) between the ages of 18 and 30 (M=22) participated.

Stimuli. Eight simple asymmetric shapes were used as central precues in a visual search task. The shapes were black, had the same area, and had an approximate diameter of 3°. The shapes' directionality had previously been determined in experiment 2.

People searched for a target cross among distractor plus signs. Distractors were made by overlaying a vertical and a horizontal bar (1.1° x 0.3° each). The target was made in the same way except that one bar was vertically displaced by 0.2°. The search stimuli were then given a random rotation on each trial. The search stimuli were black, except that a small colored circle (diameter 0.1°) was embedded in each of them. The target's circle color could be red or green and was chosen at random. The color of each distractor's circle was also randomly determined to be red or green with the constraint that there was at least one distractor disk of each color.

Design. Two sets of four shapes were used in this experiment. Half of the participants were given one set and half were given the other set. Each shape served as a predictive central precue in a visual search task. It cued one of four possible target locations (upper left, upper right, bottom left, or bottom right).

Two shapes were congruent, meaning that the shapes' inherent directionality was consistent with the direction of the target location that it cued. The other two were incongruent; they cued a target location in a direction opposite that of their inherent directionality. The two congruent shapes cued target locations on one diagonal and the two incongruent shapes cued target locations on the other diagonal (figure 3.8). The rotation of each shape was the same across all participants with the same shape set but the cue-target contingencies differed; each shape served as a congruent cue for four participants and as an incongruent cue for another four participants.

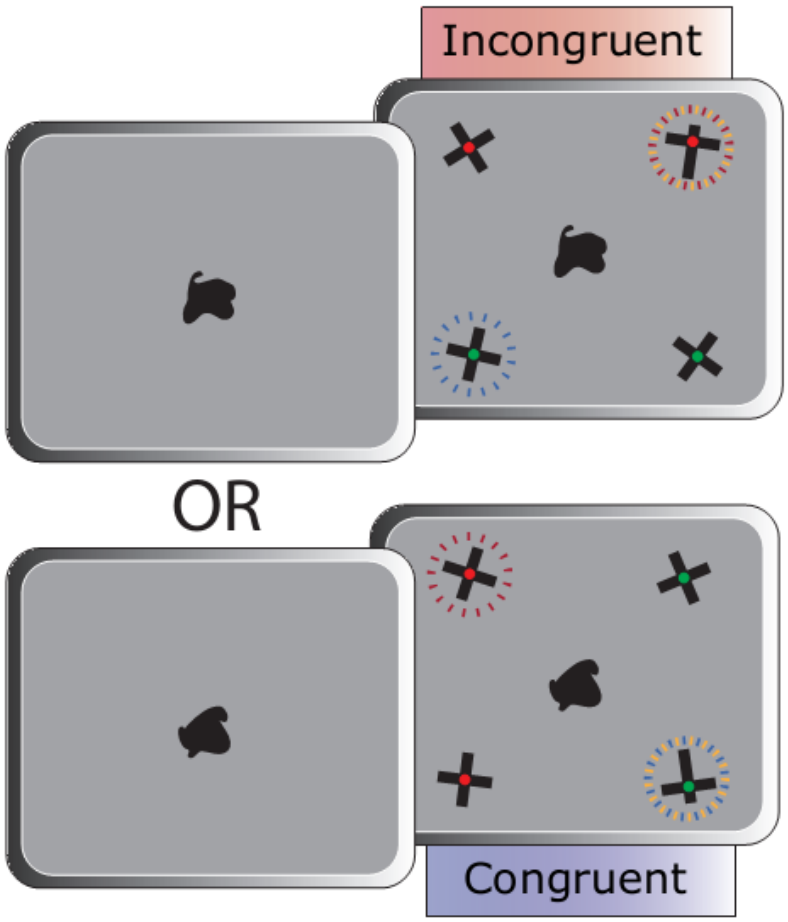

Figure 3.8. Task in experiment 4. A central shape validly cued the location of a peripheral target cross shown among distractor plus signs. Participants had to find the cross and report its central color. While all shapes provided accurate information about the upcoming target location, the cued location was congruent with the directionality of half of the shapes but incongruent for the other half. Examples of congruent and incongruent search trials are shown. Cued locations are indicated by yellow dotted circles. The locations pointed to and away from are indicated by blue and red dotted circles, respectively. No dotted circles were actually shown to the participants.

Central shape cues therefore predicted, with 100% accuracy, where peripheral targets would appear. The correctly predicted location could be congruent or incongruent with the shape's inherent directionality. Each participant completed 240 search trials spread over four blocks during a single session.

Procedure. Eye position was monitored using an EyeLink 1000 eye tracker (SR Research). The participant's gaze on a central 0.3° x 0.3° fixation square triggered the start of each search trial; she was then free to move her eyes for the remainder of the trial. The fixation square was replaced by a predictive central shape cue which was visible throughout the trial. The participant was told that a shape would appear on the screen after she had acquired fixation, and that after the shape appeared a search array would show up on the screen. After 500 ms, a square search array with three distractors and one target appeared around the central shape. The search stimuli were all shown at 11° eccentricity. The participant had to find the target and report the color (red or green) of an embedded disk by pushing the button of the corresponding color on her response box. This completely disambiguated the manual response from the directionality of the shape. The procedure is depicted in figure 3.8.

Participants were instructed to respond quickly but to try to maintain near perfect performance. Auditory feedback was given to indicate whether a response was correct or incorrect.

Results

Mean accuracy ranged from 92% to 98%. People were significantly more accurate at judging the color of a disk embedded in a target if the target was preceded by a shape cue whose directionality was congruent (M=96.2%) rather than incongruent (M=94.8%) with the target's location (paired samples t-test, $t(15)=3.257$, $p=0.005$, $d=0.81$). Error trials were not further analyzed.

Mean response time was used as a dependent measure in a repeated measures ANOVA with block (1-4) and congruency as factors. The main effects of block ($F(3,45)=9.57$, $p=5.3\times10^{-5}$, $\eta_p^2=0.39$) and congruency ($F(1,15)=15.05$, $p=0.001$, $\eta_p^2=0.50$) were significant, but the interaction between the two factors was not significant ($F(3,45)=0.98$, $p=0.409$). Overall, response times decreased over the course of the experiment. Subjects were also faster at

reporting the attributes of a peripheral target when it was in a location congruent with a central shape cue's directionality. This effect did not seem to diminish over the course of the experiment (see figure 3.9).

Because congruent and incongruent shapes were equally predictive of where a target would appear, one might have expected that the performance gap between congruent and incongruent shapes would narrow as people gained more experience with the cue-target contingencies. Although this might potentially happen with longer training, we saw no sign of it and the benefit for congruent shape cues persisted. It thus appears that people intuitively make certain associations more easily than others and that this preference is not easily erased in a single session.

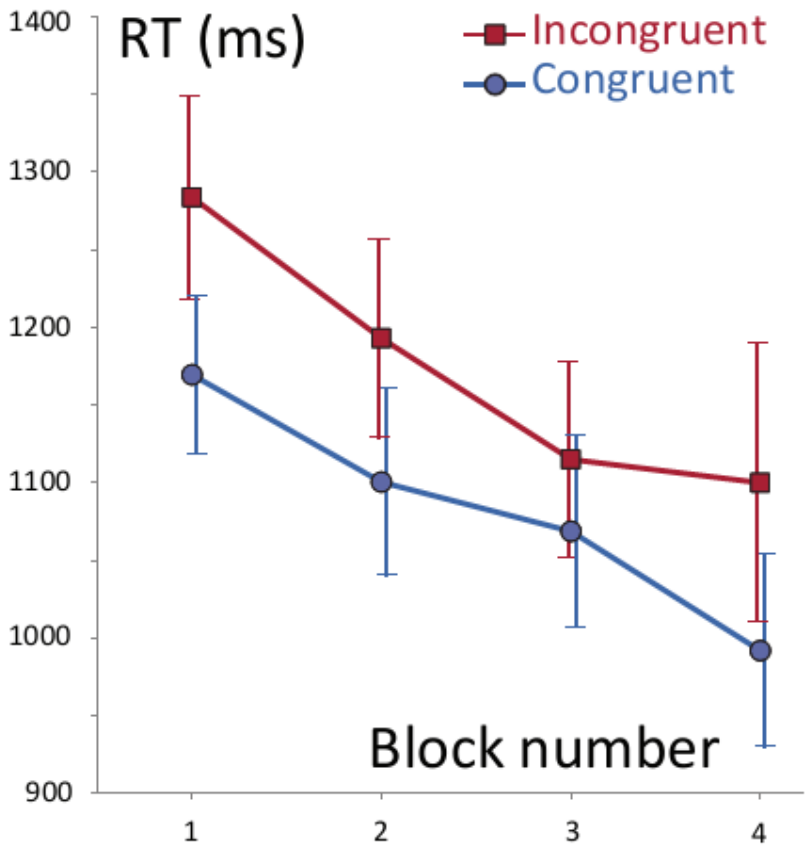

Figure 3.9. Congruency effects over the course of learning. Mean response times (RT) are shown for experimental blocks in experiment 4. A central shape cue predicted, with 100% accuracy, where a peripheral target would appear. The correctly predicted location could be congruent or incongruent with the shape's inherent directionality.

Experiment 5: Shape as a Movement Cue

So far we have shown that the shape of an object is used to rapidly and automatically extract its directionality, and that this in turn guides both overt and covert visual orienting. An unanswered question is *why* the visual system is set up this way at all. One possible reason is that the shape of an object restricts and thus predicts its movements. A snapshot of the shape of an object might therefore provide valuable information about where it may be moments later. The rules governing selective sampling of the environment should incorporate any available data, including shape, which provides prior information about where important things are going to be in the near future. Informal self-reports of participants in experiments 1 and 2 also indicated that judgments about the directionality of shapes could be related to people's perceptions about where the things were moving or heading. In experiment 5, we directly examined whether the shape-defined directionality of an object was integrated into calculations about its movement. We would reach this conclusion if people were consistently faster at judging where an object was heading if its direction of motion was congruent with the directionality derived from the object's shape.

Method

Participants. 16 people (7 women) of ages 18-54 (M=27) participated in the experiment.

Stimuli. Stimuli were the same 40 shapes used in experiment 3. The shapes were white and shown on a black background. Each shape extended approximately 1°.

Design. Each person completed 320 experimental trials in two blocks within a single session. All shapes were shown four times within each block in a random order (40 shapes x 2 shape directionalities x 2 movement directions x 2 repetitions).

Procedure. The participant was instructed to look at a fixation disk (white 0.5° diameter) at the beginning of each trial. She was otherwise free to move her eyes. The fixation disk stayed onscreen for 510 ms, and 470 ms later, participants then saw multiple copies of a particular shape lined up in a row across the screen (figure 3.10). The screen center coincided with the pivot point of the central shape (see experiment 1). The distance between corresponding points of juxtaposed copies of the shape was 2.4°. To create a moving stimulus, the row of shapes was translated 0.8°

to either the left or right every 130 ms. On any given trial, the row of shapes therefore appeared to be moving either leftward or rightward.

Shapes were shown equally often pointing to the left or the right; this directionality was defined by an independent sample of people (see experiment 2). The shapes pointed in the direction of motion on half of the trials, and pointed the opposite way on half of the trials. Shape was not a valid predictor of motion.

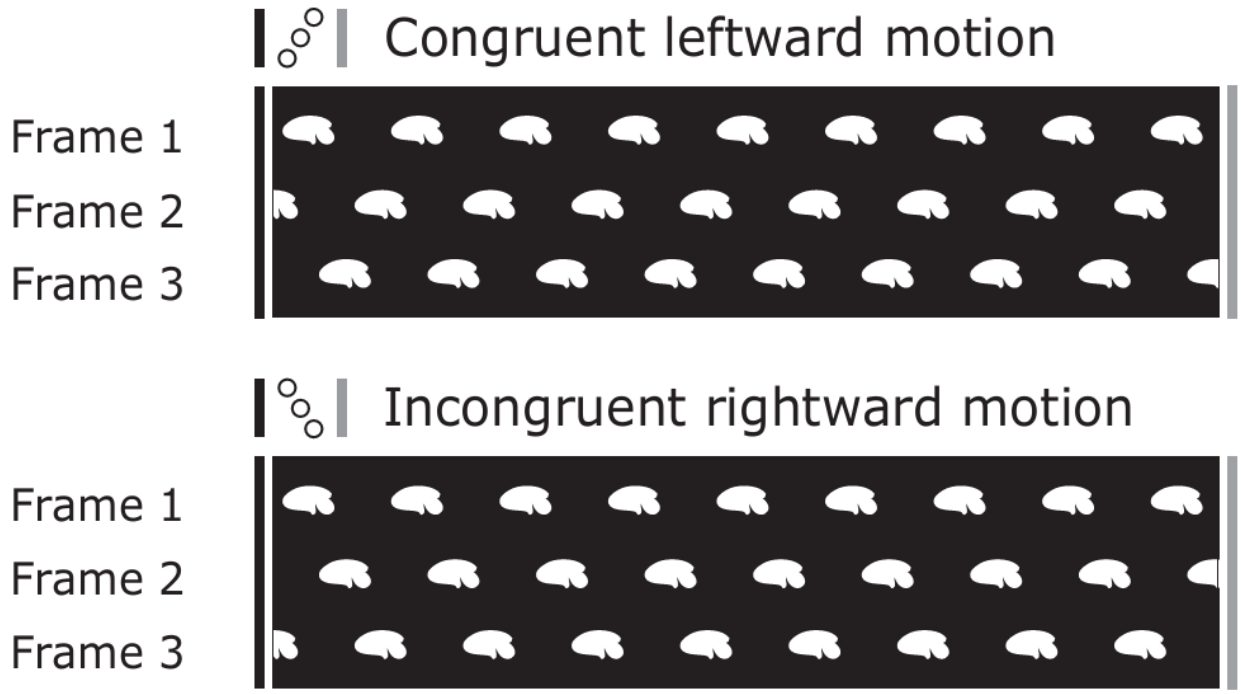

Figure 3.10. Example motion stimuli. To create a moving stimulus in experiments 5, 6, and 7, a row of shapes was translated in a direction that was either congruent or incongruent with the shapes' inherent directionality. The direction to which the example shapes are most often judged to point is indicated by a black vertical bar, and the opposite direction is indicated by a gray vertical bar.

Participants held a response button box with both hands and were told to press the left button if the shapes were moving to the left, and press the right button if they were moving to the right. A tone sounded when the participant responded. No specific feedback was provided about whether the answer was correct or incorrect.

Results

Mean accuracy ranged from 89-99%. Although accuracy was generally very high, people were significantly more accurate at judging where the shapes were going when the shapes pointed in the direction to which they were moving (congruent: M=97.9%, incongruent: M=95.0%, paired samples t-test, t(15)=4.408, p=0.001, d=1.10).

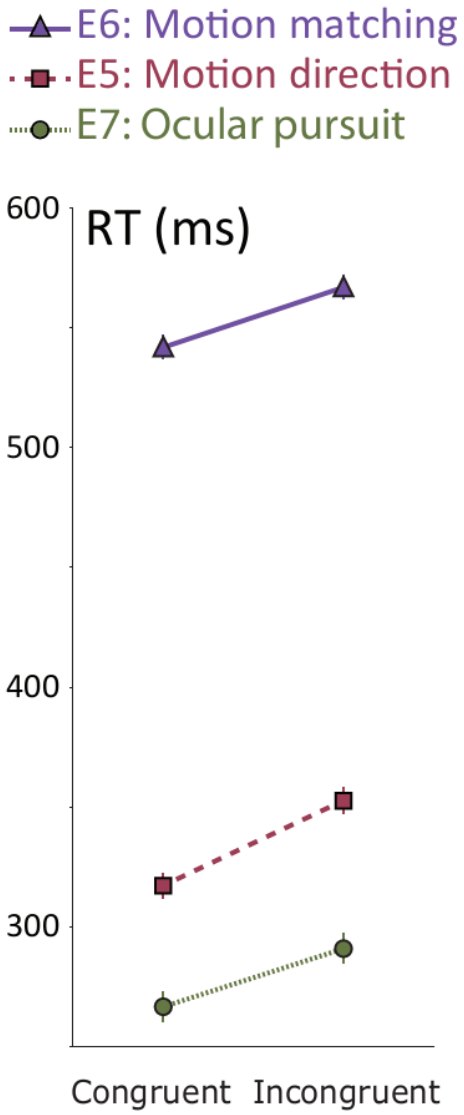

Figure 3.11. Shape as a movement cue. Mean response times (RT) are shown as a function of congruency between shape-derived directionality and direction of motion. When an object moved in the direction to which it pointed, people were faster at judging its direction of motion (Experiment 5: Motion direction), matching its motion to the motion of other objects (Experiment 6: Motion matching), and following it with their eyes (experiment 7: Ocular pursuit). Note that confidence intervals are small.

We calculated the mean response times for correct trials only. Response times were defined with respect to motion onset, which was the time of the first translation of the multi-shape stimulus. All participants were faster at judging where the shapes were going if their movement direction was congruent with their inherent directionality (figure 3.11). This effect was significant (congruent: M=317 ms, incongruent: M=353 ms, paired samples t-test, $t(15)=9.746$, $p=7.0\times10^{-8}$, $d=2.44$).

Experiment 6: Match to Motion

The results from experiment 5 were quite robust; every participant was faster at judging where a shape was going if it pointed in the direction of motion. We interpret this as evidence for the idea that the shape of an object, in particular its shape-derived directionality, is automatically integrated into movement calculations.

In experiment 6, we wanted to address two alternative interpretations. First, we wanted to rule out the possibility that any slight pixel-by-pixel differences between leftward and rightward shapes solely determined an object's supposed directionality and its behavioral effects. Secondly, it is possible that we were not seeing an effect on motion perception but rather a type of effector priming; certain shape features might afford being grasped by a particular hand, and a button press with that hand might thus become potentiated. The stimuli in experiment 5 were all very small 2D silhouettes that, if perceived as graspable at all, probably all afforded a similar pincer grip; nonetheless, we wanted to rule out this explanation.

To address these possibilities, we designed an experiment where moving shapes had a random starting position, and where manual responses were neither directly related to the direction of motion nor to the directionality of shapes. If people are still faster at judging the direction of motion of an object when it is congruent with the directionality derived from its shape, we would conclude that these alternative interpretations do not sufficiently account for our effects and that, instead, shape-derived directionality is integrated into the calculations of an object's motion path.

Method

Participants. 16 people (8 women) of ages 18 to 34 (M=22) took part in this experiment. One additional participant was excluded because of very low accuracy rate (more than six standard deviations below the mean).

Stimuli. Shape stimuli were as described for Experiment 5 with the addition of a white disk shape (diameter 0.9°).

Design. Participants completed 320 trials each in four blocks within one session. Trials were shown in a pseudo-random order. The design was fully crossed (40 shapes x 2 polarities x 2 shape movement directions x 2 disk movement directions).

Procedure. Procedure was as described for experiment 5 with the following changes. Presentation of a central fixation spot was followed by the appearance of several disk shapes that extended to the screen's edges. The horizontal starting position of the disks was random but the distance between the centers of adjacent disks was fixed at 2.4°. All disk shapes were translated 0.8° degrees every 130 ms so that they appeared to move either leftward or rightward. The disks disappeared 390 ms after their initial onset. After a 500 ms inter-stimulus interval, participants saw multiple copies of a particular novel shape. Their horizontal starting position was random but the distance between corresponding points on two adjacent shapes was always 2.4°. The shapes could point leftward or rightward, and could move leftward or rightward, as detailed in experiment 5 (see also figure 3.10).

Participants indicated whether each novel shape was moving in the same direction as the disks (match) or in a direction opposite that of the disks (non-match). Participants responded with their right hand using a two-button box. The button box was aligned so that one button was nearer the person and the other was farther away. Half of the participants pushed the closer button to indicate a match and the button farther away to indicate a non-match, and vice versa for the other half of the participants. Participants completed some practice trials with other shapes randomly picked from the rest of the original shape dataset used in experiment 2.

Results

Mean accuracy ranged from 84-100%. Participants were on average more accurate on trials where the shape's directionality was congruent with the shape's own direction of motion; this difference did not reach statistical significance (congruent: M=95.6%, incongruent: M=94.1%,

paired samples t-test, t(15)=1.676, p=0.114). Error trials were not analyzed further.

Response times were defined as the time between the novel objects' motion onset and button press. People were significantly faster when novel shapes pointed in the direction to which they were moving (congruent: M=542 ms; incongruent: M=567 ms; paired samples t-test, t(15)=7.244, $p=3x10^{-6}$, d=1.81, figure 3.11).

We regressed the objects' starting position against response time. By starting position we refer to the location of the pivot point (see experiment 1) of the central shape in the first frame *relative* to the direction of motion; for example, if the pivot is 1° to the right of the screen center, but the shape is moving leftward, then the shape's starting position is considered to be -1° relative to the motion direction. For each participant, we calculated the slope of the best fitting line (least squares method) and did so separately for congruent and incongruent trials. The participants' mean slopes for congruent (M=0 ms) and incongruent trials (M=7 ms) were neither significantly different from zero (single-sample t-test; congruent trials: t(15)=0.116, p=0.909; incongruent trials: t(15)=1.561, p=0.139), nor were they significantly different from each other (paired-samples t-test; t(15)=0.977, p=0.344). Starting position was not found to be a significant factor contributing to response times in this task.

People are therefore faster at judging the direction of movement of an object if its shape is congruent with the object's motion path. This cannot be attributed solely to pixel-by-pixel differences between leftward- and rightward-pointing objects because their starting position was randomly varied. The effect cannot be attributed to effector priming either; the effect was found even though people used one hand only and the button presses were orthogonal to the objects' direction of motion and shape-derived directionality.

Experiment 7: Shape Effects in Oculomotor Programming

Experiments 5 and 6 showed that shape can play a significant role in motion perception. However, we are especially interested in the contribution that shape information can make to action guidance, in particular oculomotor guidance, considering that shape selectivity has been found in important oculomotor centers of the brain (Janssen et al., 2008; Konen & Kastner, 2008; Lehky & Sereno, 2007; Peng, Sereno, Silva, Lehky, & Sereno, 2008; A. B. Sereno & Maunsell, 1998; M. E. Sereno et al., 2002). Given the numerous dissociations between perception and action (Goodale, 2008; Goodale & Milner, 1992; Milner & Goodale, 1995, 2010), including

oculomotor behavior (Mack, Fendrich, Chambers, & Heuer, 1985; Spering & Gegenfurtner, 2008; Spering & Montagnini, 2011; Wong & Mack, 1981), we thought it important to test whether shape affects the programming of eye movements in addition to perception. Additionally, we wished to compare the effects of novel random shapes with those of arrows, which are both familiar and highly directional, and with filled circles, which should be adirectional, to see whether shape-derived directionality mainly helps or hinders performance relative to situations in which no bias should be present. People were asked to follow a row of moving shapes with their eyes. They were free to use both saccadic and smooth eye movements for this ocular pursuit task. We expected eye movements in the direction to which the shapes were pointing to be facilitated, and eye movements in the opposite direction to be hindered.

Method

Participants. 16 people participated (7 women). Their age ranged from 18 to 24 (M=21).

Stimuli. We used 40 novel shapes, as described for experiment 5, and four additional shapes: three differently shaped arrows and a filled circle. All shapes, including the arrows and the circle, had the same area and an approximate diameter of 1°.

Design. Each person completed two experimental blocks for a total of 184 trials in random order. All directional shapes (40 novel shapes, 3 arrows) were shown 4 times each (2 motion directions x 2 shape directionalities). Circular shapes were shown on control trials (2 motion directions x 3 repetitions).

Procedure. The experimental procedure was as described for experiment 5 (see also figure 3.10) with the following changes. At the beginning of each trial, the screen center always coincided with the center of area of the central shape in each multi-shape stimulus. People were told to follow the shapes' movement (leftward or rightward) with their eyes. Eye position was tracked; a trial started once a person had acquired fixation on a central fixation spot. Instead of responding to the direction of motion with a button press, the trial ended once people's eyes reached one of two invisible circular regions, a target region in the direction of motion (correct response) or a distractor region in a direction opposite that of the real motion of the shapes (incorrect response). The circular regions were centered on the horizontal meridian at 6.0° eccentricity with a radius of 3.0°. Trials were considered valid if the subjects' horizontal eye position within the first 130 ms after stimulus onset was no further than 0.65° from the screen's

center, and vertical eye position was no further than 1.0° from the horizontal meridian throughout the trial. Furthermore, trials were considered valid only if people reached one of the circular regions within 2000 ms of motion onset. On average, 79.2% of trials were deemed valid and we base our analysis on these valid trials only.

Results

Participant's mean accuracy for novel shapes ranged from 62% to 100%. This great range of performance was surprising since the task was mainly designed to measure response time and not accuracy levels. Accordingly, here we saw a much greater difference between the accuracy in congruent (M=92.9%) and incongruent (M=84.2%) novel shape trials than in our previous experiments where accuracy was closer to ceiling. People were significantly more accurate on congruent than incongruent novel shape trials (paired samples t-test, $t(15)=3.865$, $p=0.002$, $d=0.97$). Response times were calculated relative to motion onset on correct trials only. People were significantly faster at reaching the target region, located in the direction of motion, if the novel shapes' inherent directionality was congruent with the direction of motion (congruent: M=267 ms, incongruent: M=291 ms, paired samples t-test, $t(15)=5.719$, $p=4.1\times10^{-5}$, $d=1.43$, figure 3.11). We note that the effect of congruency on both accuracy and response time remains significant even when invalid trials are included in the analysis.

We compared the effects of novel shapes with the effects of arrows. People were far more accurate when the arrows pointed in the direction of motion than if they pointed in the opposite direction (congruent: M=100.0%, incongruent: M=53.0%, paired samples t-test, $t(15)=9.918$, $p=5.6\times10^{-8}$, $d=2.48$) and almost twice as fast (congruent: M=240 ms, incongruent: M=405 ms, paired samples t-test, $t(14)=5.231$, $p=1.3\times10^{-4}$, $d=1.35$; one person had no correct incongruent trials and was therefore not included in the RT measures). People were also significantly faster and more accurate for congruent arrows than they were for congruent novel shapes, and they were significantly slower and less accurate for incongruent arrows than they were for incongruent novel shapes (paired samples t-tests, all $ps<0.003$, all $ds > 0.96$). As expected, arrows are therefore particularly effective stimuli for orienting guidance.

Finally, we compared novel shapes to filled circles (which have no directionality). The mean accuracy (M=88.9%) and response times (278 ms) for circles fell half-way in between those of congruent and incongruent novel shapes. The differences in accuracy for circles and

congruent shapes were not reliably smaller or larger than the differences in accuracy for circles and incongruent shapes ($t(15)=0.221$, $p=0.828$). Response time differences for circles and congruent shapes were not reliably smaller or larger than those for circles and incongruent shapes ($t(15)=0.129$, $p=0.899$). The effects of directionality therefore appear to be more or less symmetrical; the more congruent a shape's directionality is with the direction of motion, the faster and more accurate the oculomotor behavior, and the more incongruent a shape's directionality, the slower and more error-prone is the behavior. Shape-derived directionality appears to be a strong enough motion cue that the stimuli can be perceived to move, and are thus initially pursued, in the direction opposite that of the "real" motion. Overall, our results support the hypothesis that novel shapes have an automatic effect on oculomotor programming.

Individual Item Analysis

The possibility remained that our results were driven only by a few atypical novel shapes, with the rest of them contributing nothing to the effects. For example, it was possible that by random chance, a few of our shapes looked like arrows and that these atypical shapes were the sole driving force behind our results. To rule out this possibility, we analyzed congruency effects for individual shapes. We did so with data collected for novel shapes in experiment 3 (detection), experiment 5 (motion direction), experiment 6 (motion matching), and experiment 7 (ocular pursuit).

For experiments 3, 5, and 6, we calculated the mean response time on incongruent and congruent trials for each shape for each participant, calculated response time savings by subtracting the former from the latter, and finally found the mean response time savings for each shape across participants within a particular experiment. We included all trials regardless of people's responses to get adequate sampling of responses to each shape. Data from one participant in experiment 3 was excluded because she did not complete both congruent and incongruent trials for all of the shapes.

For experiment 7, most subjects had at least one shape with either no valid congruent trials or no valid incongruent trials; we therefore collapsed across subjects and calculated mean response times savings for each novel shape. Collapsing across subjects allowed us to include only correct trials for response time calculations and still retain enough trials for each of the novel shapes. Accuracy had a much greater range in experiment 7 than in our other experiments,

providing us with the opportunity of also looking at accuracy savings found by subtracting the percent of correct incongruent trials from the percent of correct congruent trials for each novel shape.

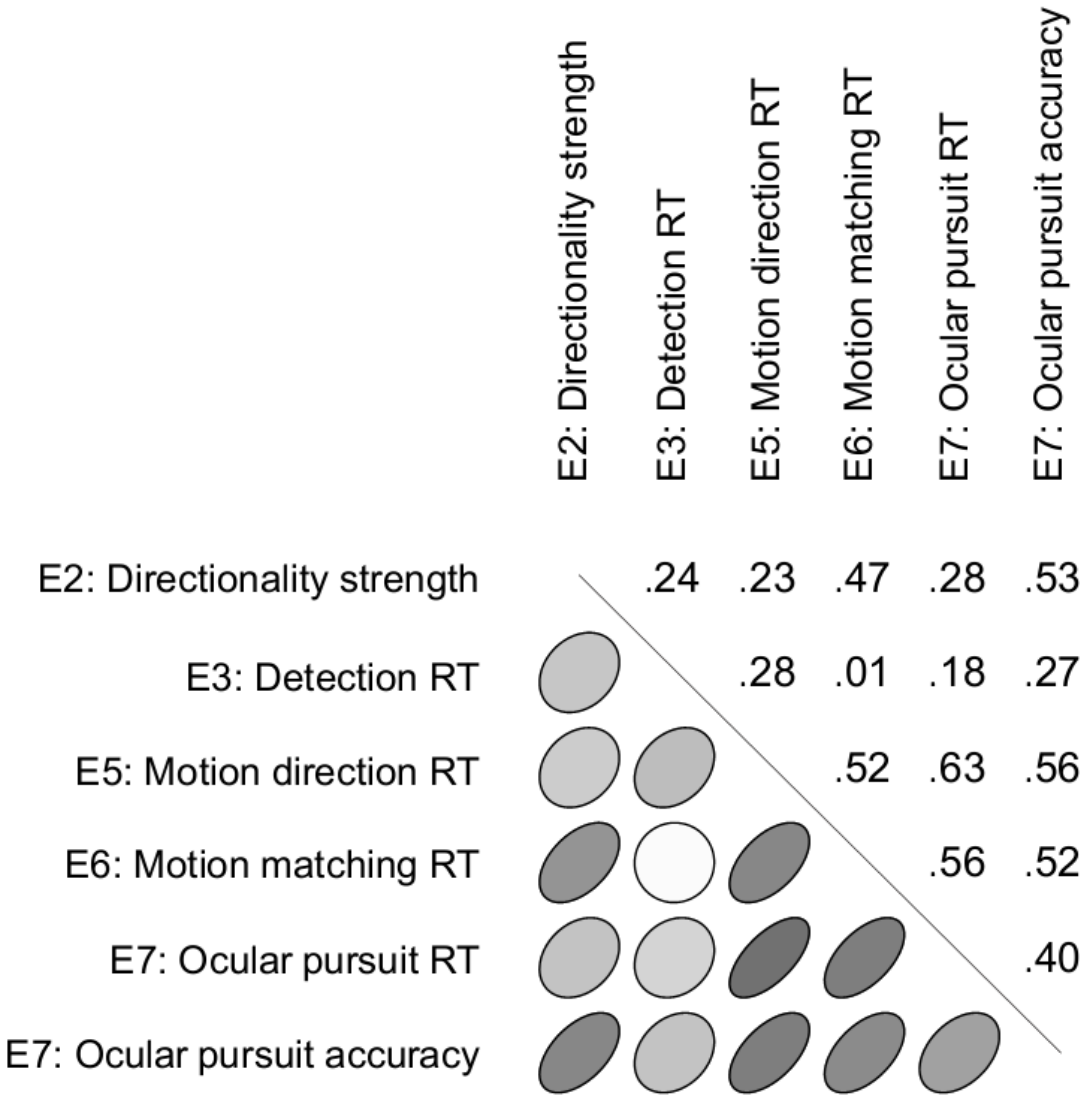

Figure 3.12. Congruency effect correlation matrix. This matrix shows the relationship between directionality strength (experiment E2) and savings measures from various tasks (experiments E3, E5, E6, and E7, summarized in Individual Item Analysis). Numbers indicate Pearson's r. Ellipses are the contours of a bivariate normal distribution with a correlation r (Murdoch & Chow, 1996).

Results

The response time savings for the 40 novel shapes were positively correlated across all four tasks (figure 3.12). Accuracy savings in the ocular pursuit task (experiment 7) were also positively correlated with response time savings from all four tasks (figure 3.12). Assuming that any one measure is a somewhat noisy estimate of the same construct, that is to say the strength of a shape-derived directional bias, we combined all five measures into a single measure of an overall congruency advantage. We did so by dividing each original savings measure by its standard deviation and then took the average for each shape across the five scaled measures.

The five original measures of savings were positively correlated with directionality strength as defined by the degree of consensus reached on the directionality of shapes in experiment 2 (figure 3.12). The overall congruency advantage scores were also significantly correlated with directionality strength ($r(38)=0.489$, $p=0.001$). As can be seen in figure 3.13, the behavioral effects were not due to a few outlier shapes; instead they were graded and related to the shapes' directionality strength. Regressing directionality strength against the congruency measure also revealed that the y-intercept (congruency advantage: -0.260) was not significantly different from 0 ($p=0.423$), indicating, unsurprisingly but reassuringly, that an adirectional shape would be expected to induce no directional behavioral bias.

The analysis of individual novel shapes shows that the stronger the directionality of a shape, the greater its behavioral biasing effects will, in general, be. This analysis also shows that our results were not driven by few very atypical shapes. Instead, congruency effects were found for a great number of shapes across various tasks. We find it parsimonious to conclude that the effects are not solely explained by resemblance to specialized stimuli such as arrows, but that the visual system instead automatically assigns directionality to many different shapes, and that this drives or biases further visual processing and guides behavior.

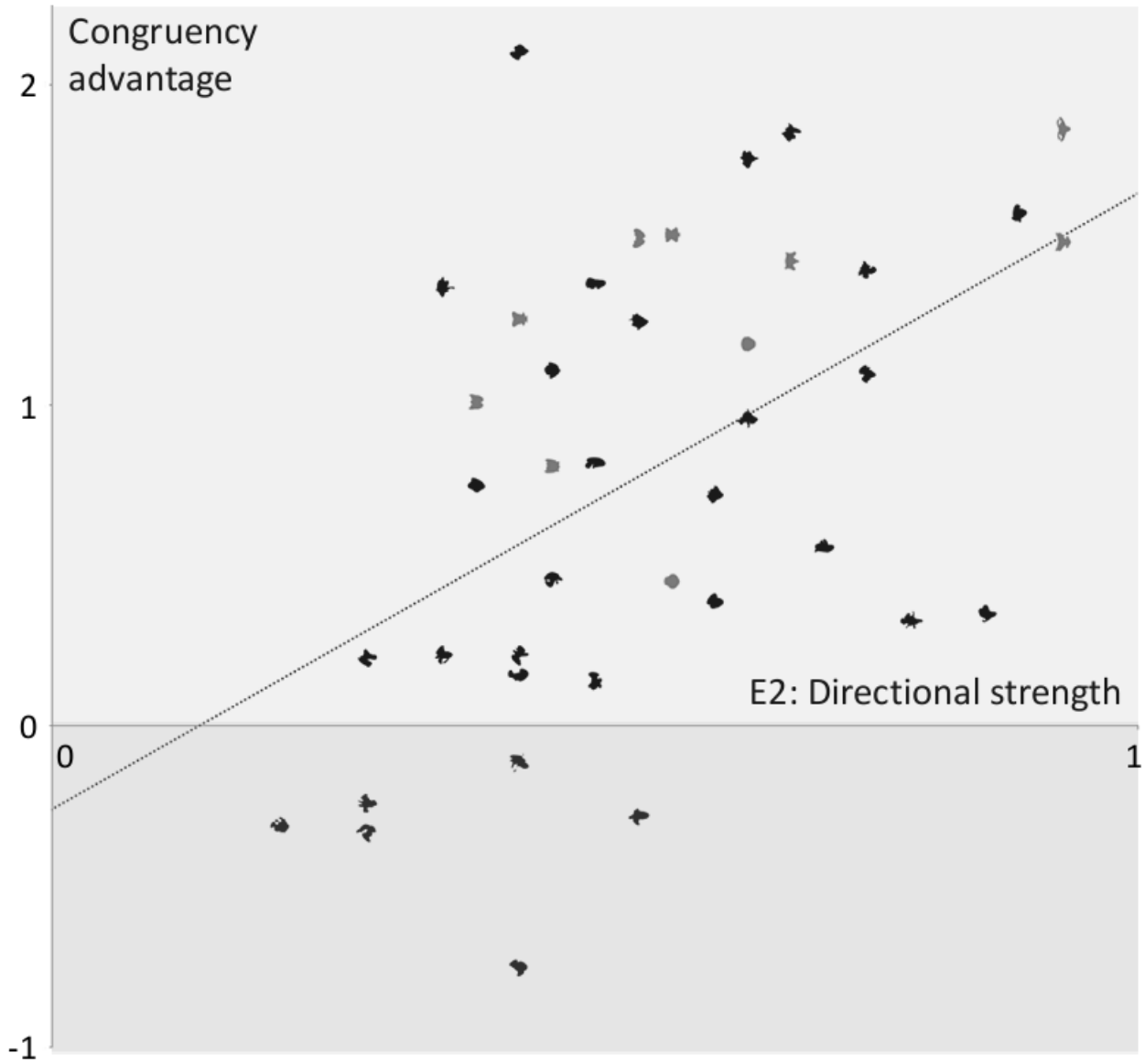

Figure 3.13. Behavioral effects of individual shapes. Each marker is in the shape of the corresponding novel object shown in experiments E3, E5, E6, and E7. Asymmetric shapes are shown in black, and symmetric shapes are shown in gray. All shapes are shown pointing to the right, as judged by participants in experiment E2. Overall, the stronger the consensus is on a shape's directionality, the greater the behavioral advantage is on congruent relative to incongruent trials.

General Discussion

We hypothesized that the visual system uses information about shape to swiftly and automatically extract the directionality of virtually any object without explicit training or learning. We explored this idea in several related experiments. A majority of randomly generated novel shapes were reliably judged to have one or more main directions (experiments 1, 2). This inherent shape-derived directionality was found to automatically guide both overt (experiment 3) and covert (experiments 4, 7) visual orienting of attention. The effect was rapid (experiment 3), resistant to experience (experiment 4), and was integrated into the assessment of an object's movement (experiments 5, 6, 7).

Our results show that an object can rapidly and automatically push attention away from itself due to its shape. This appears to be the rule and not the exception. These biasing effects are likely to be direct instead of coming about through explicit interpretation or semantics; our objects were not symbolic, they were novel and meaningless. These orienting shifts do not need to be explicitly learned or trained. They are not easily overridden or overwritten by experience, persist even when they are not useful, and are found in various tasks and situations.

The fact that our effects arise without any particular training does not necessarily indicate that experience has no role in establishing them in the first place. Indeed, previously adirectional and non-spatial visual stimuli such as color patches can start to automatically bias covert (Dodd & Wilson, 2009) and overt (Van der Stigchel, Mills, & Dodd, 2010) visual orienting once they have often been paired with a behaviorally relevant thing or action in a particular direction. The same is true for Arabic numerals where low numbers shift overt and covert visual attention to the left while high numbers shift it to the right (Dehaene, Bossini, & Giraux, 1993; Fischer et al., 2003; Fischer, Warlop, Hill, & Fias, 2004). While there might indeed be a true, spatial mental number line (Dehaene, Izard, Spelke, & Pica, 2008; Zorzi, Priftis, & Umilta, 2002), the associations between directions and these particular shapes are presumably relatively arbitrary and might come about through the cultural tradition of reading from left to right, and thus shifting your eyes and attention in the same direction (Dehaene et al., 1993; Shaki & Fischer, 2008).

The time course of learned, arbitrary visual orienting appears to be relatively slow (Fischer et al., 2003; Van der Stigchel et al., 2010) compared to the rapid effects found for novel shapes in the current study. The shape-induced biases we see arise so early that they are

presumably not dependent on recurrent feedback but likely arise from an initial bottom-up sweep of visual information. The difference might be that, unlike color patches or digits, the mapping from shape to space is not arbitrary. Colors are non-spatial and digits do not line up on any obvious spatial dimension; the shape of digits, presumably, changes completely arbitrarily going from 0 to 9. On the other hand, the directionality of a shape might lie on a dimension in a yet unknown multidimensional shape space.

Precisely documenting this shape space is beyond the scope of this paper. After participation in experiments 1 and 2, we nonetheless asked people whether they thought they had used a particular strategy or rule to complete the tasks. We summarize these informal self-reports with the hope that it will help generate hypotheses for future experiments that parametrically vary stimulus properties to address what, exactly, determines the direction of a given shape.

Several different strategies were reported. Often people reported using some geometric properties of the shapes: Direction of a large, long, tapered, or sharp protrusion, overall taper of shape, direction of the average of more than one protrusion, direction opposite a small protrusion and between two cupping protrusions, direction toward the meeting point of two tilted lines. Some reported taking into account a center of mass, like they were weighing the object, or dividing the shape into subparts and going with the direction of the part with the greatest mass or area. Some reported taking into account a general axis or an axis of symmetry. Some reported ignoring small protrusions. Some said that they had trouble judging the directionality of shapes that were blob-like or smoothly curved.

When asked, many noted that at least some of the shapes resembled real things, such as arrows, planes or flowers, but in particular animate things such as bugs, marine life, birds, space aliens, or parts of animate things such as faces, heads, mouths, antennae, tails, legs, hands and fingers. Some reported that they tended to go with the direction in which the shapes appeared to be moving or heading, or where they were facing, especially if the shapes appeared to be biological. Judgments of the shapes' animacy do nonetheless appear to be unrelated to the strength of their directionality; novel shapes that are deemed to look like some kind of existing or hypothetical creature, animal, or person, are not any more or less likely to have a strong directionality (H. M. Sigurdardottir, M. M. Shnayder, & D. L. Sheinberg, unpublished observations). Finally, some participants just reported that they did whatever felt right and that they were not consciously using any particular strategy.

In short, people seem to use various properties of objects to judge their directionality. Strategies span from taking into account particular features of the object's parts to using summary statistics of the whole shape to noting body structure and plausible movement patterns. The fact that people report so many different strategies or even no strategy at all suggests that several different form or shape characteristics might all come together to influence the judged directionality of an object, and that people might not necessarily have conscious access to the rules that they use to make such judgments. The algorithm used by the visual system to derive an object's directionality is therefore currently unknown, and there might be more than one mechanism at work.

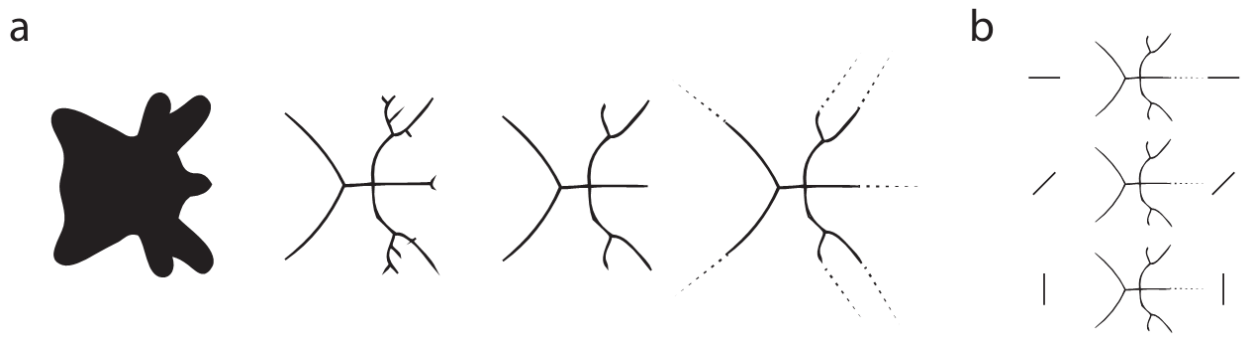

Figure 3.14. Hypothetical example of how a shape could affect target detectability. a) A shape's topological skeleton is found and pruned. Through extension of the axes of the skeleton, perhaps through rules similar to those thought to support collinear facilitation or contour completion, it is possible that the shape is grouped more strongly with targets on one side than another (here, more with a right than a left target). b) This grouping might be stronger for collinear targets (top) than non-collinear targets (middle and bottom).

We can nonetheless theorize about the mechanisms behind our results. One possibility is that our effects are driven by axis-based shape processing (see e.g. Blum, 1967: Kimia & Appear, 2003: Lin, 1996). There is already some evidence that the visual system can use axis-based shape representations and that this affects perceptual sensitivity within an object (Hung, Carlson, & Connor, 2012; Kimia & Appear, 2003; Kovács, Fehér, & Julesz, 1998; Kovács & Julesz, 1994). In figure 3.14, we have included an example shape and one scenario of how a shape's axis might affect target detectability outside its boundaries. In this example, a shape's topological skeleton is found by gradual erosion of the object's boundaries without breaking it apart (in this case using the *bwmorph* function of MATLAB's Image Processing Toolbox). The

skeleton is then pruned by cutting off its smallest branches; in computer vision, regularization of a skeleton is commonly applied to reduce noise because small changes in the boundary of an object can lead to great changes in its skeleton (Shaked & Bruckstein, 1998). The visual system might explicitly assign a direction of flow along an axis segment as supposed by some axis models such as the shock map (Kimia & Appear, 2003). Through extension of the axes of the skeleton, perhaps through rules similar to those hypothesized to support collinear facilitation or contour completion (for a review, see Loffler, 2008), it is also possible that the object is grouped more strongly with targets on one side than another. For example, the association field model assumes that contours are formed by the linking of information across neighboring neural receptive fields tuned to similar orientations (Field, Hayes, & Hess, 1993; Ledgeway, Hess, & Geisler, 2005). The fact that directionality affects the perception of motion is at least consistent with the role of collinear facilitation since it may subserve not only contour formation but appears to influence motion perception as well; the speed of collinear sequences is overestimated (Seriès, Georges, Lorenceau, & Frégnac, 2002) and a vertical line moved horizontally toward a stationary horizontal line can be misinterpreted as the movement of the latter line since it is parallel to the direction of motion (Metzger, Spillmann, Lehar, Stromeyer, & Wertheimer, 2006). Real-world objects can be viewed as spatiotemporal events, and their motion can be thought of as a change in the objects' boundaries over both space and time. It might therefore be expected that mechanisms which support boundary completion in space might also be involved in boundary completion over time, where the shape of an object's current boundaries is used to predict its future state.

If mechanisms such as those underlying collinear facilitation and contour integration are involved, then a number of predictions can be made (although there is some disagreement on the relation between collinear facilitation and contour integration, see Loffler, 2008; Williams & Hess, 1998). First, the biasing effects of a shape might be expected to interact with the qualities of the target. The greatest facilitation would be expected for targets that are collinear with the directionality of the shape, and little facilitation would be expected for targets orthogonal to or tilted relative to the shape's directionality (Polat & Bonneh, 2000; Polat & Sagi, 1994). Second, there might be no congruency effects when an orthogonal distractor is placed between a target and a shape (Dresp, 1993). Third, because the detectability of a contour increases with the number of elements making up a path (Braun, 1999), a "daisy chain" of shapes could induce

stronger congruency effects than a single shape; this is one possible reason why the effects in our motion paradigms (experiments 5-7) seemed particularly robust. Fourth, the congruency effect would be expected to change in magnitude and even sign with the relative distance between the shape and the target (Polat & Sagi, 1993, 1994). Fifth, the congruency effect should reach its peak at a later time point with increased distance between the shape and the target (Cass & Spehar, 2005). It would in general be very interesting to document further how shape-induced biases develop in both space and time, where target detectability would be probed not just at several different time points but at various distances and directions from a shape.

In addition to, or instead of, the mechanisms discussed above, the rules linking shape and space might be more explicitly derived from the complex but non-random way in which the shape of an object restricts its movements and therefore its probable future location. Our stimuli were two-dimensional silhouettes, but real objects exist and move in a fully three-dimensional world. If an object is assigned a directionality for the purpose of predicting its future location, then real-world objects might have a directionality defined in not just two but three dimensions. If all other things are equal, an object is likely to move in a path of least resistance to air flow. Preliminary work from our laboratory suggests that directional judgments might be related to a shape's aerodynamic properties. The greater the consensus reached on the directionality of a shape, the better its path of least resistance approximated the shape's empirically defined directionality (S. Boger and S. M. Michalak, unpublished observations). Further work on the role of aerodynamics is warranted. The current results show that the visual system is able to link the appearance of an object with its possible path of motion. Directional information derived from shape can be used to guide the eyes and attention to the object's future location so that it can be tracked, examined, and acted on.

Our experiments were based on the hypothesis that the shape of an object affects the weights given to locations in a spatial priority map (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Itti & Koch, 2001). Overt and covert visual attention would be guided to the location of peak activity within the map once activity reaches a particular threshold, and this attentional orienting signal would in turn bias other processes such as motion perception (Cavanagh, 1992; Stelmach, Herdman, & McNeil, 1994; Treue & Maunsell, 1996). Such a tight link between shape, attentional priority, and motion perception is biologically plausible; posterior parietal regions which play an important role in target selection and visual orienting (Andersen, Snyder,

Batista, Buneo, & Cohen, 1998; Arcizet, Mirpour, & Bisley, 2011; Bisley & Goldberg, 2010; Colby & Goldberg, 1999; Gottlieb, Kusunoki, & Goldberg, 1998; Silver, Ress, & Heeger, 2005) are furthermore selective for the shape of objects (Janssen et al., 2008; Konen & Kastner, 2008; Lehky & Sereno, 2007; Red et al., 2012; A. B. Sereno & Amador, 2006; A. B. Sereno & Maunsell, 1998) and their activity is predictive of the perceived motion direction of ambiguous motion stimuli, even to a greater extent than activity within the classical motion regions MT and MST (Williams, Elfar, Eskandar, Toth, & Assad, 2003). The behavioral experiments reported here were also directly prompted by our own electrophysiological work where we recorded activity of single neurons within these posterior parietal regions (discussed in chapter 2). This line of research showed that rapid and automatic neural responses to novel visually presented shapes, responses which previously had no known function, could be directly tied to the allocation of spatial attention and eye movements.

There are, however, other possibilities. For example, motion processing might have a primary role, where shape directly affects the calculation of motion and overt and covert attention is then guided in the direction of movement. Also, if the shape and the target are grouped into one perceptual whole, then the effects reported here might not strictly be considered only spatial and the enhancement for the target to which a shape points could be closely related to object-based attention (Driver & Baylis, 1989; Duncan, 1984; Egly, Driver, & Rafal, 1994). The mechanisms behind the behavioral results reported here need to be further studied.

It is worth noting that earlier attempts to find effects of shape directionality on orienting apparently failed (Zusne & Michels, 1964). Zusne and Michels (1964) did not find evidence for the idea that people would preferentially follow the main direction of a shape with their eyes. The discrepancy between this and the current study could be due to the fact that Zusne and Michels (1964) did not empirically define the shapes' directionality. Wolfe, Klempe, and Shulman (1999) also failed to find evidence for the hypothesis that varying an object's polarity, which roughly corresponds to our idea of directionality, led to efficient visual search. They concluded that there is little evidence for the preattentive processing of an object's polarity. We do not think that our results necessarily contradict those of Wolfe et al. (1999). As these authors themselves acknowledge, it is hard to interpret negative findings. More to the point, we are not claiming that directionality is an attribute that supports efficient visual search, or an almost instantaneous readout (e.g. pop-out) of some particular information. This kind of fast information

detection might be fundamentally different from what we are talking about here, which is a stimulus-driven, rapid and seemingly automatic shift in information sampling. An object's directionality also pushes attention away from the object itself. There is no specific reason why a strongly directional shape should *itself* be particularly rapidly detected in a visual search.

The affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010) states that sensory information leads to the specification of current action possibilities which then compete with each other for ultimate selection for behavior (for uses of the word affordance, see also Gibson, 1986; McGrenere & Ho, 2000). Our results could be interpreted within this framework, as the shape of an object may lead to the specification of orienting affordances, or the possible ways to look and pay attention, some of which have a greater chance of being selected than others. Regardless, it is conceivable that the biases we report here can act as a front end to more traditionally defined affordance effects that involve physical interactions through reach and grasp (Bub & Masson, 2010; Cisek, 2007; Tucker & Ellis, 1998; for further discussion on the possible interplay between attention and affordance, see e.g. Anderson, Yamagishi, & Karavia, 2002; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Riggio et al., 2008; Vainio, Ellis, & Tucker, 2007). Under most circumstances, people look where they are about to act, so eye gaze precedes hand movements both inside the laboratory and in real-world tasks (Ballard et al., 1992; Hayhoe, 2000; Hayhoe & Ballard, 2005; Land & Hayhoe, 2001; Land, Mennie, & Rusted, 1999). Eye orientation also directly affects where people reach (Enright, 1995), and dorsal stream posterior parietal regions important for saccade and reach planning appear to share a common eye-centered coordinate frame (Cohen & Andersen, 2002). Visual attention also appears to be directed from one object to another when familiar, manipulable objects are positioned in a manner that facilitates their interaction, such as when a hammer and a nail are seen together in a position that would allow the hammer to strike the nail (Green & Hummel, 2006; Riddoch et al., 2011; Roberts & Humphreys, 2011; Yoon, Humphreys, & Riddoch, 2010). It would be very interesting to see what, if any, role the effects reported here play in such paired-object affordance effects.

While eye and hand are clearly coupled, orienting biases such as those that we see here are in all likelihood not identical to reach and grasp affordances. It is not clear if unfamiliar 2D silhouettes on a computer screen afford reaching and grasping at all, and the effects are found even when the eyes and not the hands are used as effectors. It is also reasonable to assume that

shape-induced orienting biases are evoked by objects beyond reach, such as birds in flight. In some cases, orienting biases might even directly oppose reach and grasp affordances. For example, when using a bottle or teapot, people tend to look at the bottle mouth or spout, or at the container into which they are pouring, instead of looking at their hands or the point of contact (Hayhoe, 2000; Land et al., 1999). Certain types of affordances and the effects reported here might nonetheless share the fundamental property of being "recognition free", involving a more-or-less direct coupling between vision and action.

Being able to circumvent recognition does not necessitate complete isolation from it. Within the field of computer vision, the detection of a shape's orientation is an often-used image preprocessing step applied before image registration and recognition (El-Sayed, Abdel-Kader, & Ramadan, 2010), and a number of algorithms have been developed to automatically detect the orientation and/or directionality of shapes (Cortadellas, Amat, & de la Torre, 2004; El-Sayed et al., 2010; Lin, 1996; Martinez-Ortiz & Zunic, 2010; Tzimiropoulos, Mitianoudis, & Stathaki, 2009; Zunic & Rosin, 2009; Zunic, Rosin, & Kopanja, 2006). The systematic and rapid extraction of an object's directionality could also serve a role in human object recognition (see e.g. Leek & Johnston, 2006; Maki, 1986) by facilitating the search for and alignment to an existing object template or model.

In some cases, especially when objects are unfamiliar or if they are seen from an unfamiliar viewpoint, visual recognition is viewpoint-dependent (Rock, 1973; Tarr & Bülthoff, 1998; Tarr & Pinker, 1989; Tarr, Williams, Hayward, & Gauthier, 1998). When a previously seen object is encountered again from another viewpoint, the new object instance (or, alternatively, an internal reference frame; Robertson, Palmer, & Gomez, 1987) is thought to go through an iterative transformation, such as a mental rotation (Carpenter & Just, 1978; Shepard & Metzler, 1971; Zacks, 2008; but see Farah & Hammond, 1988; Hayward, Zhou, Gauthier, & Harris, 2006; Turnbull & McCarthy, 1996) or alignment (Huttenlocher & Ullman, 1987), that orients the observed object with either a previously seen view or a privileged, canonical view (Jolicoeur, 1985, 1990; Jolicoeur & Landau, 1984; Palmer, Rosch, & Chase, 1981; Robertson et al., 1987; Tarr & Pinker, 1989). Stored object views have a particular orientation and handedness (Tarr & Pinker, 1989) which can be thought of as having a specific directionality. The shortest path between a new and stored view could conceivably be calculated based on the angular difference between the directionality of the stored and observed object.

If a sufficient match to a stored representation is not found, directionality could be used to standardize the building of a new representation that is not completely dependent on the viewpoint from which an object happens to be first seen; the visual input could for instance be transformed and stored in a canonical directionality, such as upright. There indeed appears to be a favored view from which an object is most readily recognized (Palmer et al., 1981; see also Blanz, Tarr, & Bülthoff, 1999; Turnbull, Laws, & McCarthy, 1995), and damage to the parietal cortex can lead to specific deficits in recognizing objects from other, more unconventional views (Warrington & Taylor, 1973). The loss of the ability to automatically extract an object's directionality could hypothetically lead to such a deficit by preventing the correct normalization to a canonical object representation. The suggested route to recognition is just one of potentially many possible ways to identify an object (Jolicoeur, 1990; Lawson, 1999; Vanrie, Béatse, Wagemans, Sunaert, & Van Hecke, 2002), some of which may not rely in any way on a shape's directionality. Independent of these speculations, here we have shown that shape influences processes beyond recognition, and these findings may provide insight into why object form may be processed in parallel throughout the visual brain.

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CHAPTER FOUR

A tale of two coordinate systems

Introduction

Dozens of cortical regions in the primate brain are devoted to the processing of visual information (Van Essen et al., 2001). Many of these regions are topographically organized so that neurons that respond maximally to visual information in nearby spatial regions cluster together and form an organized map (Kaas, 1997; Van Essen, Newsome, & Maunsell, 1984; Wandell & Winawer, 2011). Several brain regions seem to represent spatial locations in a retinotopic coordinate frame (Gardner, Merriam, Movshon, & Heeger, 2008; Golomb & Kanwisher, 2012; Wandell & Winawer, 2011). This is perhaps not surprising since doing so requires no additional coordinate transformations from the original, native space; light first gets transduced into neural signals in the retina of the eye, and where exactly it falls depends on the center of gaze. Such maps in posterior visual regions can be revealed by the use of simple visual stimuli, such as rotating flickering monochromatic checkerboard patterns, which periodically stimulate a particular part of the retina (Engel, Glover, & Wandell, 1997; Engel, Rumelhart, Wandell, & Lee, 1994; for a review of retinotopic mapping, see Wandell & Winawer, 2011).

Several anterior regions also appear to show at least a crude topography but might be more particular about the types of stimuli and tasks that effectively reveal the maps. For example, maps in the human intraparietal sulcus regions IPS1 and IPS2 were first revealed by the use of a covert attentional task (Silver, Ress, & Heeger, 2005) and a memory guided saccade task that relied not just on passive visual stimulation but on active memorization of spatial locations to which overt and covert visual attention needed to be allocated (Schluppeck, Glimcher, & Heeger, 2005).

In some circumstances, it might be beneficial to code locations in another type of coordinate system that is independent of one's eye position. The brain indeed seems capable of such coordinate transformations (for reviews, see e.g. Andersen, Snyder, Li, & Stricanne, 1993; Graziano, 2001). There have been reports of the coding of visual information in several egocentric coordinate systems where locations are represented relative to parts of one's own body. These include eye-centered (Batista, Buneo, Snyder, & Andersen, 1999; Mullette-Gillman, Cohen, & Groh, 2005; Pouget, Ducom, Torri, & Bavelier, 2002; Vetter, Goodbody, & Wolpert, 1999), head-centered (Andersen, Essick, & Siegel, 1985; Mullette-Gillman et al., 2005; M. I. Sereno & Huang, 2006; Soechting, Tillery, & Flanders, 1990; Zhang, Heuer, & Britten, 2004), body-centered (Carrozzo, McIntyre, Zago, & Lacquaniti, 1999), shoulder-centered (Soechting et

al., 1990), and joint-centered (Pouget et al., 2002) coordinate systems. Such egocentric coding is probably particularly beneficial for action planning since visual information becomes available in the space of the body part which needs to be moved.

However, there are situations where it might be advantageous not to code where things are relative to one's own body, but relative to other objects in the world. When one watches a soccer match, one might want to keep track of where the ball is relative to the goal, where it is relative to the players, where the players are relative to each other etc. At any given time point, the ball, the goal, and each player all occupy a particular location on the viewer's retina, and several brain regions will inherit and keep that retinotopic frame of reference. High level regions, however, might have the capability to further transform this visual information into a stimulus-centered or object-centered coordinate system that is more suitable for the situation. A stimulus-centered reference frame is centered on the middle of a target stimulus regardless of its egocentric position, while an object-centered reference frame is centered on an object, but its left-right orientation is based on the object's canonical orientation (Medina et al., 2009); an object-centered reference frame therefore rotates with the rotation of an object, while a stimulus-centered reference frame does not. Note that this distinction is not always made and different nomenclature may be used (Walker, 1995).

Object-centered or stimulus-centered coding has been reported for some cortical regions (for a review, see Olson, 2003). Much work has focused on the supplementary eye fields (SEF) in the dorsomedial frontal cortex of the macaque monkey. Single neuron activity in SEF can depend on whether monkeys make an eye movement to the left or right of a bar, regardless of where the bar is relative to the center of gaze (Olson & Gettner, 1995). SEF neurons are mainly selective for "contralateral" stimulus-centered space, i.e. the SEF in the left hemisphere mostly contains neurons that prefer stimulus-centered rightward locations, and neurons in the right SEF predominantly prefer left stimulus-centered space (Olson & Gettner, 1995; Olson & Tremblay, 2000; Tremblay, Gettner, & Olson, 2002). However, stimulus-centered coding of SEF neurons is weak before the monkeys have been explicitly trained on a stimulus-centered task (Olson, 2003), begging the question of whether such a coding scheme is mainly of importance after weeks or months of training. The monkeys' task also involved the execution of motor commands so it is possible that SEF is involved with stimulus-centered coding of saccadic eye movements but does not otherwise encode the visual stimulus-centered location of a target.

We are mainly interested in the coding of perceptual and attentional stimulus-centered information, in particular the possible role of the dorsal visual pathway in such spatial representations. It has been proposed that coding strategies within the dorsal visual pathway are largely based on viewer-centered or egocentric coordinate systems (Goodale & Milner, 1992). These types of representations can presumably be more easily used by the motor system to calculate the movements of the appropriate effector, or body part, to e.g. reach for, grasp, or look at an object. There is nonetheless some evidence that object-to-object relational coding relies on the parietal cortex.

Parietal damage sometimes brings on constructional apraxia (Black & Bernard, 1984; Black & Strub, 1976; Gainottil, 1978) where patients have difficulties in assembling, drawing, or otherwise constructing objects despite being physically able to perform the movements needed for the task. This ability depends on relational coding of object parts. Parietal damage can also lead to neglect (Medina et al., 2009; Vallar & Perani, 1986) where one side of space is unattended or ignored (figure 4.1). While the patients in many cases neglect the contralesional egocentric space, such as the space left of the sagittal midplane of the trunk and the line of sight (Bisiach, Capitani, & Porta, 1985), neglect can also manifest itself in an allocentric or extra-personal reference frame (Bickerton, Samson, Williamson, & Humphreys, 2011; Bisiach, Perani, Vallar, & Berti, 1986; Driver & Halligan, 1991; Farah, Brunn, Wong, Wallace, & Carpenter, 1990; Ota, Fujii, Suzuki, Fukatsu, & Yamadori, 2001; Tipper & Behrmann, 1996; Walker & Young, 1996; for a review, see Walker, 1995).

For example, Bickerton et al. (2011) tested patients with acute unilateral brain lesions on an “apple cancellation task” where they were presented with 150 line drawings of upright apples that were either complete or had a gap on their right or left side. The participants were asked to cross out all the complete apples while ignoring incomplete ones. Right-hemisphere patients were more likely than left-hemisphere patients to show a page asymmetry in detecting full apples, and the side of their lesion predicted the sign of the asymmetry (classified as egocentric contralesional neglect). The lesion side predicted the sign of an object-based or stimulus-based asymmetry as well; patients with right hemisphere damage were more likely to ignore gaps (i.e. mark apples as complete) on the left side of apples (36% of left-hemisphere patients) than the left side of apples (3%), and patients with left hemisphere damage were more likely to ignore gaps on the apples’ right side (18% of left-hemisphere patients) than they were with gaps on the left

(7%). Compared to left-hemisphere patients, right-hemisphere patients also tended to show greater object-centered or stimulus-centered spatial asymmetries where they falsely marked incomplete apples with gaps on one side as being complete.

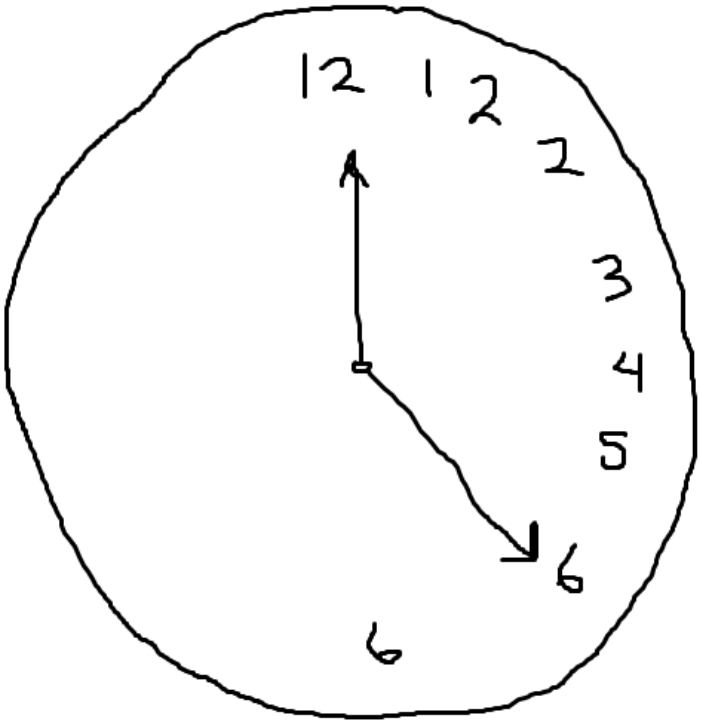

Figure 4.1. Hemispatial neglect. When asked to draw a clock, a patient with left hemispatial neglect might ignore one side of the clock (image reproduced from a patient's drawing, see http://www.scholarpedia.org/article/Hemineglect). Most patients neglect a part of egocentric space, but some patients also appear to suffer from object-centered or stimulus-centered neglect.

The difference between subtypes of neglect does not appear to be clear-cut and the same patient's neglect might manifest itself in both egocentric and extra-personal or allocentric reference frames (Bickerton et al., 2011; Walker, 1995). It is possible that these patients suffer from damage to brain regions that simultaneously code for locations both in egocentric and object- or stimulus-centered reference frames. There are, however, reports of dissociations of neglect as manifested in these different spatial reference frames (Gardner et al., 2008; Marsh & Hillis, 2008).

Damage to the posterior inferior temporal (BA 37) and lateral occipital areas (BA 19) has been reported to be most predictive of stimulus-centered neglect (Medina et al., 2009), and

damage to the posterior middle/inferior temporal regions (BA 37) was found to be most predictive of object-centered neglect. Another study indicated that the extent of damage in the right superior temporal cortex (BA 22) predicted the severity of stimulus-centered neglect (Shirani et al., 2009). Neither of these studies found parietal damage to be a significant independent predictor of stimulus-centered neglect, and both conclude that allocentric coding of space (stimulus- or object-centered) involves the ventral visual pathway, while egocentric coding of space relies on the dorsal visual pathway.

Of course, absence of evidence is not evidence for absence. Studies of normal human populations and non-human primates seem to potentially indicate a role for the dorsal visual pathway/parietal cortex in the stimulus-centered coding of space. Fink, Dolan, Halligan, Marshall, and Frith (1997) contrasted an egocentric task with an object- or stimulus-based attentional task. In the egocentric task, participants were asked to report whether a line with an attached square was on the left or right of fixation, while in the stimulus-centered task, they were asked to report whether the square was attached to the left or right side of the line. Relative to the control condition, both tasks activated the left and right medial superior parietal cortex, the left lateral inferior parietal cortex, the left prefrontal cortex, and the cerebellar vermis, leading the authors to conclude that the parietal cortex is important for both object-based (or stimulus-based) and egocentric visual attention. These authors also reported that the object-based task evoked greater activity than the egocentric task in the left striate and prestriate cortex (BA 17/18) although the reason for that is unclear.

Similar studies were done by Galati et al. (2000) and Neggers, Van der Lubbe, Ramsey, and Postma (2006) where subjects judged whether a vertical bar was on the left or right of the midline of their bodies (egocentric task) or left or right of the midpoint of a horizontal line whose egocentric location could vary (stimulus-centered task). Relative to a control task in Galati et al. (2000), the stimulus-centered task activated the right posterior parietal cortex and the right frontal premotor cortex. Neggers et al. (2006), on the other hand, concluded from their study that spatial coding within the parietal cortex was involved in judging locations from an egocentric perspective but reported (amongst other areas) a parametric influence of stimulus-centered locations on activity evoked by egocentric judgments in the right medial temporal gyrus within the lateral occipital complex (LOC) which is most often considered a part of the ventral visual stream (Malach et al., 1995).

Still other studies do point to some involvement of the parietal cortex in tasks that involve stimulus-centered judgments. Fink et al. (2000) report an involvement of the right superior posterior and right inferior parietal lobe in a line bisection judgment task, as well as low level visual regions and the cerebellar vermis. In a visuomotor task, Honda, Wise, Weeks, Deiber, and Hallett (1998) report the right posterior parietal cortex (BA 7 and 19) as being one of the regions activated to a greater degree when subjects used an object-centered rule than when they used a screen-centered rule. The authors speculate that this activation could reflect the use of the visual information in spatially guided movements. Relative to a control task, Committeri et al. (2004) found that several parietal regions were activated when participants had to judge which one of two objects was closer to a reference object. These included the superior parietal lobule and the intraparietal sulcus, extending posteriorly to occipital regions. When compared to the control task, one region in the lateral occipital-temporal (in the right inferior temporal gyrus and left inferior occipital gyrus) was found to be solely active in this stimulus-centered task, and not in either a viewer-centered or a landmark-centered task.

Of course, finding that regions are activated during a task that involves relational judgments does not necessarily indicate that the region actually carries information about stimulus-centered or object-centered spatial locations. Studies that have tried to answer such a question have given somewhat equivocal results. Vicente-Grabovetsky, Mitchell, Carlin, and Cusack (2011) used MVPA to try to dissociate retinotopic (or eye-centered) and object-based coordinates but found no indication of such objectotopy. They speculate that either object-based reference frames do not exist or that they are only used in particular tasks or conditions. Golomb and Kanwisher (2012) again used MVPA to try to separate retinotopic and spatiotopic location coding, spatiotopic here indicating relative to the world, but found that all detectable location information was retinotopic. These authors speculate that such representations might only be represented implicitly. It is still possible that their subjects might have tried to solve their tasks by using strategies that relied more on the coding of retinotopic locations, leaving the construction of explicit stimulus-centered location coding unnecessary.

We are particularly interested in understanding more about spatial representations of higher level visual regions, especially within and around the intraparietal sulcus. Several topographic maps have been found within and close to the intraparietal sulcus (Schluppeck et al., 2005; M. Sereno, Pitzalis, & Martinez, 2001; Silver & Kastner, 2009; Silver et al., 2005). They are named

IPS0 (also called V7), IPS1, IPS2 and so forth. The human regions IPS1 and IPS2 are likely homologues for the lateral intraparietal area (LIP) of the macaque because these regions show various functional similarities (Konen & Kastner, 2008a, 2008b; Silver & Kastner, 2009).

In light of our previous results, these regions were of primary interest to us. We have shown that the shape of objects carries information about salient spatial locations (chapter 3), and that this kind of information is represented by LIP neurons (chapter 2). However, there were some indications that our shapes were not solely affecting attentional priority signals in a retinotopic map since directional biases persisted even though the absolute spatial location of the shapes was varied (chapter 3, experiment 6). LIP in monkeys and IPS1/IPS2 in humans have also been reported to show tolerance to object transformations, such as translation and scaling (Konen & Kastner, 2008b; A. Sereno & Maunsell, 1998). If such results are to be reconciled with our interpretation of shape selectivity in LIP and its human homologue as supporting orienting guidance, then it needs to be shown that these regions can represent space not just in pure retinotopic coordinates but can code for space relative to the location of the object itself. When an object is, say, translated to a new retinotopic location, it could still guide your eyes and attention to the same relative location in space. Sabes, Breznen, and Andersen (2002) reported that they found very little evidence for an object-centered coding scheme for LIP neurons and concluded that LIP coded for saccade target locations in retinotopic coordinates. However, as pointed out by the authors themselves, this conclusion relies on the assumption that the monkeys used an object-based strategy to solve their task. They also rotated their reference object in the picture plane which should affect an object-centered reference frame but not a stimulus-centered frame. It is still possible that LIP neurons (and neurons in IPS1 and IPS2) can code for locations in a stimulus-centered reference frame.

The main focus of the current study is to explore stimulus-centered coding in visual regions, particularly dorsal stream regions, and compare these stimulus-centered regions to both retinotopic and object selective regions. For this, we developed a novel stimulus with the goal of simultaneously mapping stimulus-centered space, retinotopic space, and object selectivity in human visual areas (like in most fMRI studies, we do not distinguish between a retinotopic coordinate frame and other egocentric frames of reference, e.g. head-centered). Besides saving time, simultaneous mapping gives a unique glimpse into the extensive parallel processing of the brain. The implicit assumption is often made that a brain region represents some one particular

type of information, whether it is retinotopic location, object-centered location, objects, faces, places, colors, etc. There are almost certainly regions that do not lend themselves to this taxonomy and simultaneously code for many different things at once.

To make sure that stimulus-centered spatial locations were task-relevant, we specifically asked people to constantly monitor where one object was located in relation to another. We did this because object-centered coding requires transformations from the native retinotopic space, and it is not clear whether the brain automatically performs such complex computations unless the task cannot be solved in any other way. Both objects constantly changed retinotopic locations, thus further discouraging the strategy of coding for the objects' locations in a retinotopic coordinate frame. The objects were also always shown on a colorful, rotating, flickering checkerboard wedge. When the object that the subjects monitored was in a particular stimulus-centered location, all other stimulus-centered locations equidistant to the reference object were therefore also occupied by a visual stimulus. All of the corresponding locations on the retina should therefore be stimulated more or less to the same degree, making it even less likely that retinotopic coding of location is of much use in the task. The experiment was controlled by an open source, platform independent program that we intend to make freely available for use and modification.

We expected to be able to map several retinotopic regions and that their boundaries would agree with already published data. Severe distortions of maps in lower level visual regions that are already known to have a clear retinotopy would indicate a failure of maintaining fixation despite fixation training. We also expected to find both dorsal and ventral object selective regions in higher level visual cortex. We finally expected some higher level visual regions, but not lower level visual regions such as the primary visual cortex, to show indications of stimulus-centered location coding. We were particularly interested in looking at the contribution of parietal cortical areas, such as IPS1 and IPS2, to such stimulus-centered coding. We also expected left higher level visual regions to mainly prefer right stimulus-centered space, and right higher level visual regions to mainly prefer left stimulus-centered space, and we through it possible that this asymmetry was greater in the right hemisphere. Finally, we were interested in seeing where these stimulus-centered and retinotopic regions were relative to object selective regions in the dorsal visual pathway. We thought it likely that they would show considerable

overlap; one possible reason for object selectivity in the dorsal visual pathway is that objects, unlike scrambled objects, have an orienting affordance and thus provide spatial information.

Materials and Methods

Participants

16 people (four women) between the ages of 18 to 29 years (mean: 24) participated in the experiments. They were all right handed and had normal or corrected-to-normal vision. They all gave their written consent prior to behavioral training and scanning. The experimental protocol was approved by Brown University's Institutional Review Board.

Stimuli

The mapping stimulus (see figure 4.2) used in this study was to a large extent modeled by that of Swisher, Halko, Merabet, McMains, and Somers (2007) which successively mapped retinotopic regions of the parietal cortex. The stimulus consisted of a flickering checkerboard pattern. The pattern extended to the borders of a square region (22 x 22 degrees of visual angle) whose upper and lower borders reached the edges of the display. Adjacent checks were of an opposite brightness so bright and dark checks alternated. The checks changed from light to dark at a frequency of 4 Hz. At the same frequency, each check was randomly assigned a new color. The radius of the checks increased logarithmically with eccentricity. Each individual check had a fixed location. The entire flickering checkerboard was viewed through a 90º wedge-shaped aperture which smoothly rotated around a central fixation spot. The central fixation spot was a filled white circle (diameter ~0.2 degrees of visual angle) with an inner smaller black circle (diameter ~0.1 degrees of visual angle). The wedge started at the top position at the beginning of each run and rotated clockwise or counterclockwise, depending on the run, at a fixed rate. The wedge went full circle every 48 seconds (0.02 Hz).

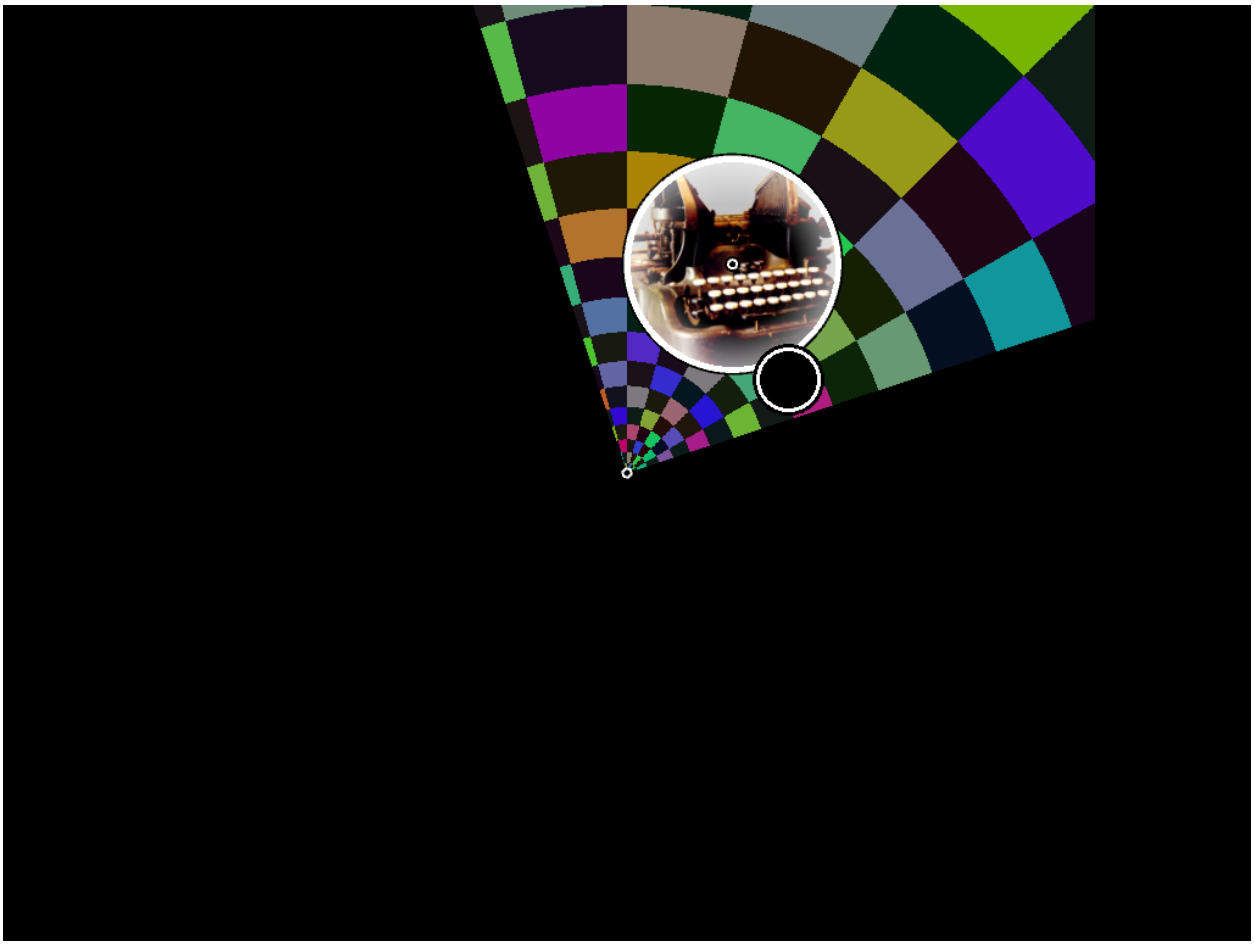

Figure 4.2. An example frame showing the mapping stimulus.

84 color images of objects on a gray background and phase scrambled versions of those same images were used as secondary stimuli. Images in each run were randomly picked without replacement until all images had been shown. The image order was then shuffled again in the same manner. An image was displayed in the center of the primary wedge stimulus, and smoothly moved at the same rate as the wedge. The images were shown through a Gaussian aperture within a circular region (from now on referred to as “the planet”). A spot identical to the central fixation spot was always shown in the center of the planet. The center of the planet had a fixed eccentricity of ~6 degrees of visual angle.

Each image was shown for one second. The stream of images was continuous (stimulus onset asynchrony 0 ms). Objects and scrambled objects were shown in 10 second blocks each. 10 objects therefore alternated with 10 scrambled objects (0.05 Hz).

A black circle (from now on referred to as “the moon”) with a diameter of ~2 degrees orbited the planet at a fixed rate. One orbit took 30 seconds. The distance between the center of the planet and the center of the moon was fixed at ~3 degrees. At the beginning of each run, the moon’s started in the upper-most position relative to the center of the planet. It orbited the planet in the same direction (clockwise or counterclockwise) as the direction in which the planet orbited the central fixation spot.

Procedure

The subjects were asked to maintain fixation at all times while constantly monitoring where the moon was positioned relative to the center of the planet. All participants practiced the task outside the scanner. 12 out of 16 participants were trained to maintain fixation while doing the task prior to their scanning session. Their eye movements were recorded and auditory feedback was given whenever their eyes strayed more than 1.75 degrees away from the screen’s center. The participants were trained to a criterion; they practiced the task in four-minute blocks until their eyes only deviated from the allotted central spot a maximum of two times in a block. Most participants reached this criterion within one or two blocks. The remaining four participants were all experienced psychophysical subjects. They were tested in the same way after their scanning session. None of them deviated from the allotted central location more than two times during a block. Eye position was monocularly recorded at 1000 Hz. The analog signal was sampled and digitized at 200 Hz. Calibration was done by asking people to saccade to small targets at several locations on the screen.

Each participant’s fMRI session started with a high-resolution anatomical scan, followed by four 8-minute functional mapping runs. Mapping runs took eight minutes each. Each person completed two clockwise runs, one of which started with an object block and the other which started with a block of scrambled objects, and two counter-clockwise, again one starting with objects and the other starting with scrambled objects. Run order was counterbalanced between participants.

MRI Data Acquisition

Scanning was done on a 3T Tim Trio MRI system (Siemens Medical Solutions, Erlangen, Germany) using a 32-channel head coil. High-resolution anatomical images were collected using

an MEMPRAGE (Multi-Echo Magnetization-Prepared Rapid-Acquisition Gradient Echo) sequence (TE=1.64 ms, 3.50 ms, 5.36 ms, and 7.22 ms, TR=2530 ms, FOV=256 mm, 176 slices, voxel size=1 mm^3). Whole-brain functional images were acquired using an EPI sequence (TE=28 ms, TR=2500 ms, FOV=192 mm, 42 slices, voxel size: 3 mm^3) with an interleaved slice acquisition. The scanner automatically discarded two pre-steady-state volumes at the beginning of each acquisition sequence. The start of the acquisition of the first additional volume triggered the beginning of stimulus presentation.

MRI Data Analysis

High resolution anatomical images were used to reconstruct the cortical surface using FreeSurfer's (http://surfer.nmr.mgh.harvard.edu) automatic cortical reconstruction pipeline (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). Data from the mapping runs were analyzed using AFNI (Cox, 1996; Cox & Hyde, 1997) and SUMA (Saad, Reynolds, Argall, Japee, & Cox, 2004). Raw data from mapping runs were analyzed in two different ways, one for the purpose of doing retinotopic mapping, and the other for linear regression.

For retinotopic mapping, data was first slice timing corrected. The EPI volumes and the anatomical were registered to the fourth volume of the first EPI series. The time series was mapped to a standard mesh model (mesh density linear depth: 141) of the subject's cortical surface and were smoothed on the surface to a target blur level of 6.0 mm FWHM. The time series were then fast Fourier transformed (FFT) so that the power and the phase at the fundamental frequency of the wedge (0.02 Hz) could be estimated for each surface node. Each phase corresponds to a particular polar angle of the checkerboard wedge. Borders of a continuous strip of retinotopic areas from the primary visual cortex to IPS1 were then drawn by hand on the inflated cortical surface (V1, V2d, V3d, V3A, V3B, V7/IPS0, and IPS1). Map boundaries for other IPS regions were unclear for many subjects and were thus not included in the ROI analysis.

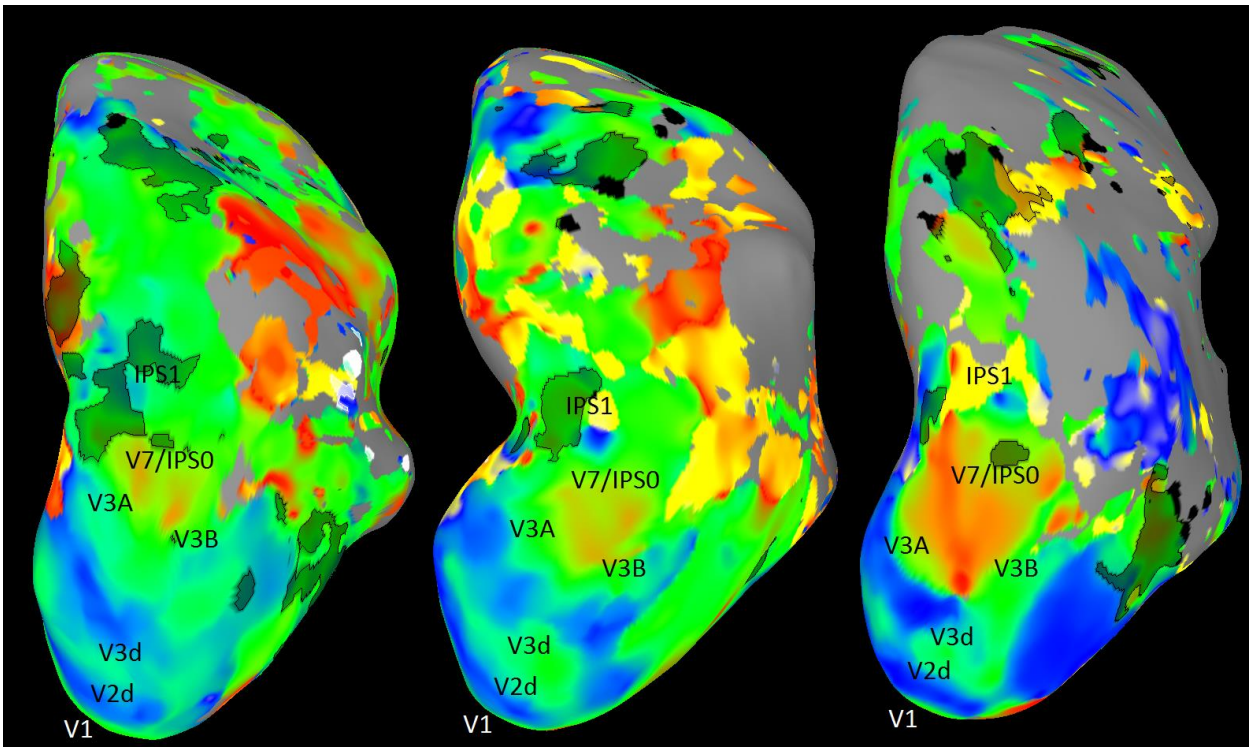

Figure 4.3. Three example subjects. The subjects' dorsal cortical surface (right hemisphere, inflated view) is shown. For clarity, indicators of gyri and sulci are not shown. Black outlined regions (transparent for retinotopic regions, otherwise solid color) responded more to object-centered left positions than to object-centered right positions. White outlined regions (transparent for retinotopic regions, otherwise solid color) responded to a greater degree to object-centered right positions than to object-centered left positions. The stimulus-centered contrast is thresholded at p=0.001, uncorrected, no clustering. These stimulus-centered regions are shown on top of the subjects' retinotopic maps (blue: retinotopic down; green: retinotopic left; red: retinotopic up; yellow: retinotopic right).

For the latter analysis, data were slice timing corrected and despiked. The anatomical was aligned to the first functional volume. Functional volumes were registered to this first functional volume as well. The functional data was then mapped to a standard mesh model (mesh density linear depth: 141) of the subject's cortical surface.

For exploratory analysis of the entire cortical surface, the functional data was smoothed on the surface to a resulting blur level of 6.0 mm FWHM. Each voxel's time series was then scaled to have a mean of 100, where a change of one unit represented 1% change. Ordinary least squares (OLSQ) regression was then performed. We included the following conditions: Left wedge (any time the entire wedge was on the left side of the screen; 12 second duration), right wedge (any time the entire wedge was on the right side of the screen; 12 second duration), left moon (any time when the moon's center was anywhere between 36° and 144° relative to the

center of the planet; 9 second duration; 0° is up relative to the center of the planet, 90° is left, 180° is down, and 270° is right), right moon (when the moon's center was between 216° and 324° relative to the planet's center), objects (10 second duration), and scrambled objects (10 second duration).

Ideal reference time series for each condition were constructed by modeling them with boxcar functions (1 for the stimulus duration, otherwise 0). An incomplete gamma function was then convolved with the boxcar functions. The reference time series were included in the model as regressors of interest. Six estimated motion parameters (three translation movements, three rotation movements) and their derivatives were used as nuisance regressors in the model. The mean, and linear, quadratic, cubic, and quartic trends across time were also removed. Volumes with excessive motion were censored (the derivative of motion parameters was found and the square root of the sum of squares was taken; if this Euclidean norm exceeded 0.3 mm, then the TR was not included). Volumes were also censored if over 10% of voxels in the volume were outliers, as defined by the AFNI program 3dToutcount. Beta coefficients for each regressor of interest were computed.

For each participant, the difference between the beta values for the right and left moon conditions (right moon – left moon contrast) was calculated for each surface node in the standard surface mesh (Argall, Saad, & Beauchamp, 2006). Single group t-tests were then done on these beta differences. Single group t-tests were done in the same manner for right wedge – left wedge, and for objects – scrambled objects.

For ROI analysis, the ROIs drawn on the surface were projected back into volume. Only voxels belonging to the pial surface were included. The same was done for the functional time series from each run. The time series for the voxels belonging to each ROI mask were then averaged at each corresponding time point, and the resulting mean time series was scaled to have a mean of 100, and a unit size of 1% signal change. Linear regression was performed on each of these ROI time series in the same manner as described above. The beta coefficient differences (right moon – left moon) for each ROI were used in further analyses.

Results

ROI analysis

For each participant, beta coefficient differences for stimulus-centered coding (percent signal difference for right moon – left moon) were found for each ROI in each hemisphere (figures 4.3 and 4.4). IPS1 was our primary region of interest so we first performed single group t-tests, one for the IPS1 region in each hemisphere, against the null hypothesis of no difference between the right and left moon conditions. No significant difference was found for IPS1 in the left hemisphere ($t(15) = -0.723$, $p = 0.481$) but a significant difference was found for the IPS1 region in the right hemisphere ($t(15) = -2.176$, $p = 0.046$). The difference between the IPS1 regions in the two hemispheres was also significant (paired samples t-test, $t(15) = -2.578$, $p = 0.021$). The right hemisphere IPS1 thus responded to a greater degree when the moon was to the left of the planet than when it was to the right of the planet, and did so to a greater extent than the IPS1 region in the left hemisphere.

A repeated measures region (V1, V2d, V3d, V3A, V3B, V7/IPS0, and IPS1) x hemisphere (left and right) ANOVA was then performed. Degrees of freedom were Greenhouse-Geisser corrected in cases where Mauchly's test of sphericity was significant.

No main effects of region were detected ($F(2.553, 38.296) = 0.822$, $p = 0.473$); there were thus no overall detectable differences in the degree to which different ROIs (collapsing across hemispheres) preferred the right moon over the left moon. There was, however, a main effect of hemisphere ($F(1, 15) = 7.958$, $p = 0.013$). Right hemisphere regions in general tended to prefer left stimulus-centered space, and left hemisphere regions tended to prefer right stimulus-centered space, and the difference between the hemispheres was significant. It should be noted that this effect appears to be mainly driven by the right hemisphere's preference for left stimulus-centered space (see figure 4.4).

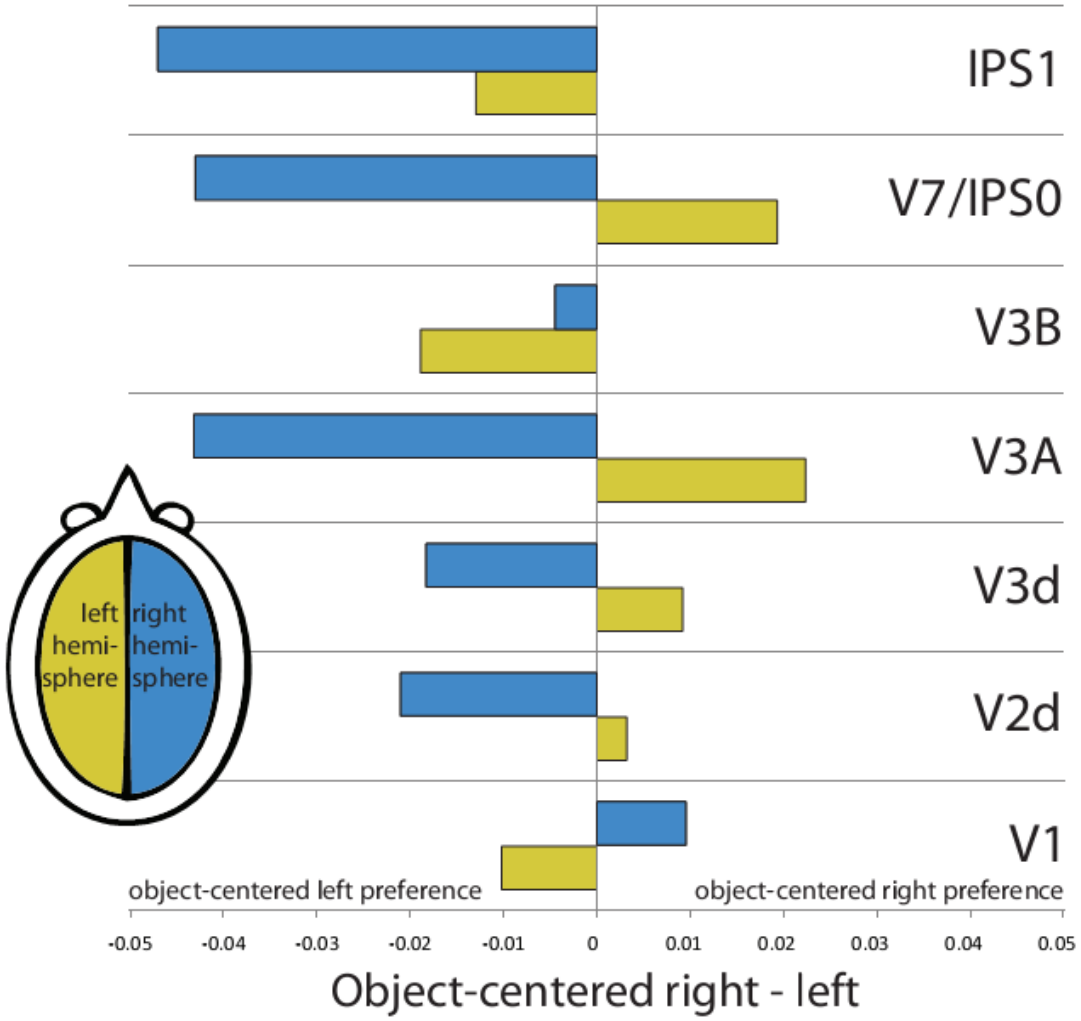

Figure 4.4. The average % signal change per ROI for the right minus left moon contrast.

Finally, there was a significant region x hemisphere interaction ($F(3.186, 47.797) = 5.563$, $p = 0.002$; see also figure 4.4). To quantify this interaction, we followed this up with paired samples t-tests for each individual region where we compared the stimulus-centered location preference for the two hemispheres. This hemispheric difference in percent signal change can be interpreted as the degree of stimulus-centered "contralateral" preference (positive scores) and stimulus-centered "ipsilateral" preference (negative scores). From now on, we will just refer to it as stimulus-centered contralateral preference. As can be seen in figure 4.5, the low level regions V1 ($p = 0.333$) and V2d ($p = 0.142$) did not show a difference in their stimulus-centered contralateral preference, and neither did V3B ($p = 0.469$). V3d, however, did show such

an effect, where the right hemisphere had a greater preference for left stimulus-centered space (compared to right stimulus-centered space) than the left hemisphere did ($p = 0.046$). The same was true for V3A ($p = 0.001$), IPS0 ($p = 1.7 \times 10^{-4}$), and IPS1 ($p = 0.021$). It should be noted that two regions, V3A and IPS0, survive a fully Bonferroni corrected alpha value of 0.0071.

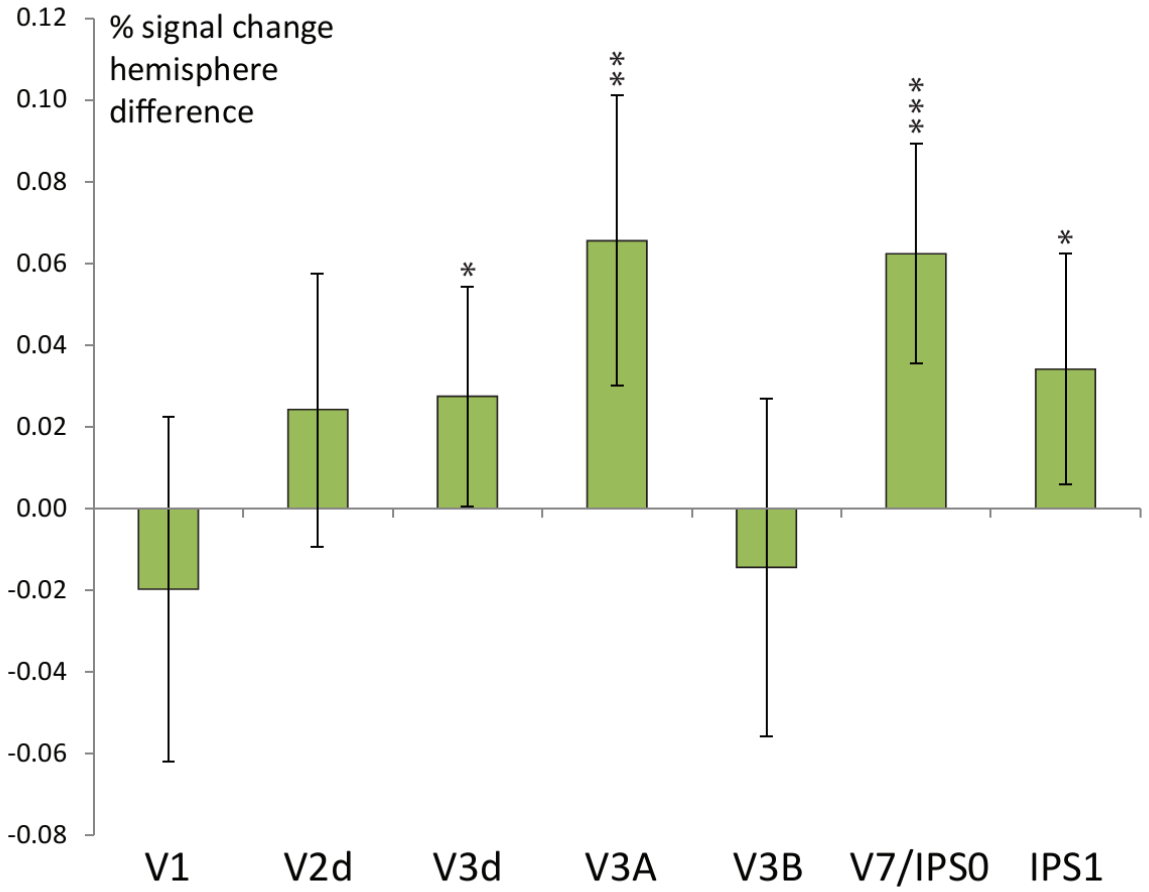

Figure 4.5. Stimulus-centered coding by cortical region. The average signal difference between right and left stimulus-centered locations (right moon – left moon) was found for each retinotopic region in each hemisphere. For each region, the difference scores for the two hemispheres were then compared. For each region, the difference between the scores for the two hemispheres was taken (left hemisphere – right hemisphere). This hemispheric difference in percent signal change can be interpreted as the degree of stimulus-centered "contralateral" preference (positive scores) and stimulus-centered "ipsilateral" preference (negative scores; null hypothesis, no preference; * indicates $p < 0.05$; ** indicates $p < 0.005$; *** indicates $p < 0.0005$). Error bars represent 95% confidence intervals.

We also compared the degree of stimulus-centered contralateral preference between the different cortical regions with additional paired samples t-tests. As can be seen in table 4.1, V2d,

V3d, V3A, IPS0, and IPS1 all show stimulus-centered contralateral preference that is significantly greater than that of V1. V3A, IPS0, and IPS1 also have a stimulus-centered contralateral preference that is of a significantly greater magnitude than that of V3B. V3A and IPS0 have greater stimulus-centered contralateral preference than does V3d. The contralateral preferences of V3A, IPS0, and IPS1, while significantly different from both zero and from the control region V1, cannot be statistically determined to be different from one another. Note that even with a full Bonferroni correction ($\alpha = 0.0024$), V3d, V3A, and IPS0 still all have a significantly greater stimulus-centered contralateral preference than does the control region V1.

Table 4.1. Comparison of stimulus-centered "contralateral" preference between retinotopic cortical regions. Significant differences are noted with stars (* indicates $p < 0.05$; ** indicates $p < 0.005$; *** indicates $p < 0.0005$). Next to the stars is the name of the region whose stimulus-centered contralateral difference is the greater of the two.

	V1	V2d	V3d	V3A	V3B	V7/IPS0	IPS1
V1		V2d*	V3d**	V3A***		IPS0**	IPS1*
V2d	V2d*						
V3d	V3d**			V3A*		IPS0*	
V3A	V3A***		V3A*		V3A*		
V3B				V3A*		IPS0**	IPS1*
V7/IPS0	IPS0**		IPS0*		IPS0**		
IPS1	IPS1*				IPS1*		

Analysis of the whole cortical surface

In addition to the main region-of-interest analysis, we performed an exploratory analysis of the entire cortical surface. The results of three t-tests for the right minus left moon contrast, the right – left wedge contrast, and the objects – scrambled contrast are shown together on an inflated standard-mesh brain (figures 4.6 and 4.7; results are thresholded at $p < 0.05$, two-sided, uncorrected).

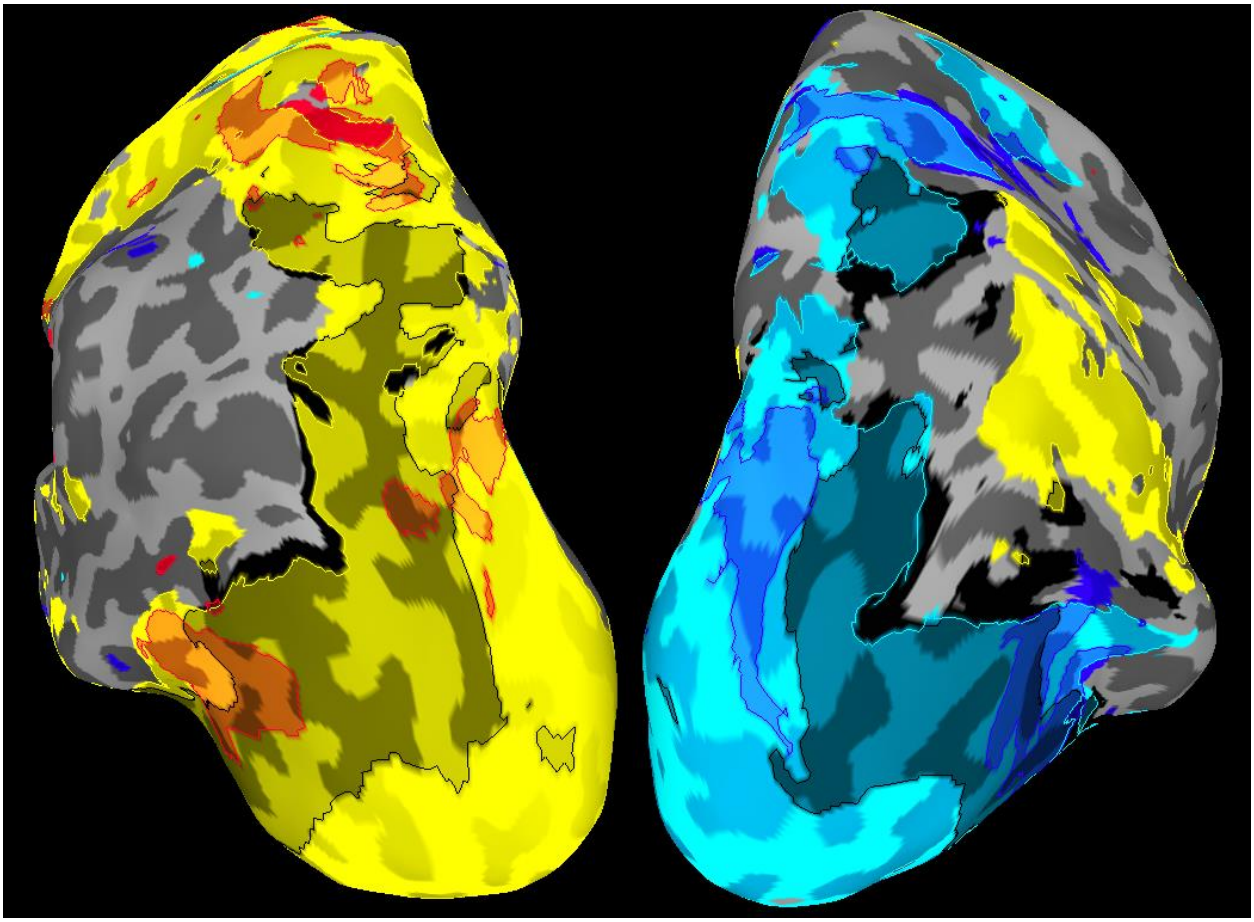

Figure 4.6. Exploratory analysis of the whole cortical surface – dorsal stream. Cyan: Left retinotopic preference. Yellow: Right retinotopic preference. Blue: Left stimulus-centered preference. Red: Right stimulus-centered preference. Black: Object preference. Not shown: Scrambled preference. Colors are blended in overlap regions.

There are several things to be noted. First of all, two clusters of a size greater than 500 mm^2 are found in each hemisphere for the stimulus-centered right – left moon contrast. Both have a stimulus-centered contralateral preference. The more posterior cluster covers parts of the ascending limb of the inferior temporal sulcus (anterior occipital sulcus), the inferior occipital sulcus and gyrus, the middle occipital gyrus, and the middle occipital and lunate sulcus. The other more anterior cluster is found mainly in the superior parietal cortex but extends into the intraparietal and postcentral sulci. Both clusters are mainly found within regions that have a contralateral retinotopic preference although, interestingly, the anterior cluster extends into regions that are flanked by regions with a contralateral retinotopic preference but they themselves show no consistent retinotopic contralateral or ipsilateral preference.

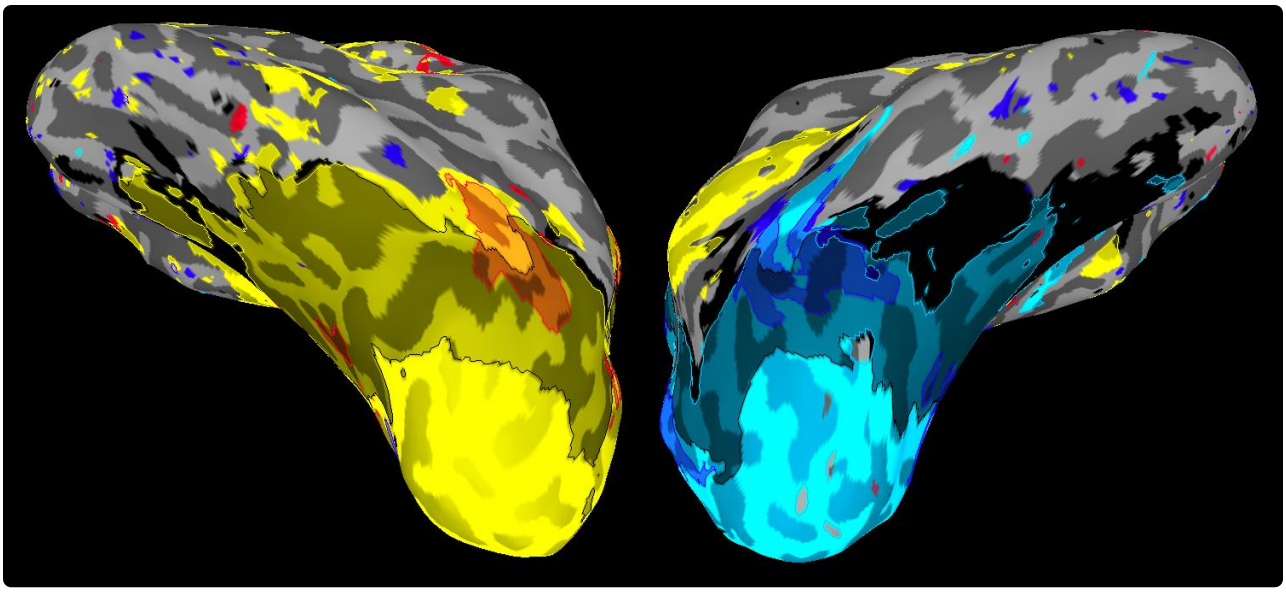

Figure 4.7. Exploratory analysis of the whole cortical surface – ventral stream. Cyan: Left retinotopic preference. Yellow: Right retinotopic preference. Blue: Left stimulus-centered preference. Red: Right stimulus-centered preference. Black: Object preference. Not shown: Scrambled preference. Colors are blended in overlap regions.

A second thing to note is that object-selective regions form a continuous strip extending from anterior ventral regions all the way to high level dorsal stream regions in the intraparietal sulcus (figures 4.6 and 4.7). On the ventral surface, especially in the right hemisphere, object selective regions extend more anteriorly than the regions that show a consistent contralateral preference for retinotopic space. Object-selective regions also partially overlap with the posterior stimulus-centered clusters.

Object-selectivity in dorsal regions, unlike in ventral regions, appears to be restricted to regions with a contralateral retinotopic preference. Interestingly, while a large extent of the dorsal stream is found to be object-selective, these object-selective regions overlap very little with regions showing stimulus-centered coding of space. Object-selective regions are found to be more lateral and posterior than areas that show stimulus-centered coding.

Discussion

We used a novel mapping stimulus to simultaneously map retinotopic space, stimulus-centered space, and object selectivity in the human brain. Retinotopy, especially in lower level

visual regions, agreed well with published data on retinotopic mapping. The current work additionally supports the idea that higher level regions of the dorsal stream can code for space in a stimulus-centered, non-egocentric reference frame. The retinotopic coordinate system nonetheless tended to dominate, and most regions showing the capability of coding for space in stimulus-centered coordinates were confined within areas of cortex that also showed a preference for contralateral retinotopic space.

Object selective regions in the dorsal stream, unlike those of the ventral stream, were also found almost completely within the boundaries of regions with a contralateral retinotopic preference. Stimulus-centered regions and object selective regions in the dorsal visual pathway were, however, largely separable. There is an apparent distinction between dorso-dorsal regions that prefer objects and contralateral retinotopic space, on the one hand, and dorso-ventral regions that prefer contralateral stimulus-centered and contralateral retinotopic space, on the other hand. While somewhat surprising, it has already been suggested based on anatomical data from macaques that the dorsal visual pathway should be further subdivided into a dorso-dorsal stream and a dorso-ventral stream that might serve different functions (Rizzolatti & Matelli, 2003).

A region-of-interest analysis confirmed that the intraparietal region IPS1 shows a contralateral stimulus-centered preference. This is mainly true for the right IPS1 which shows a preference for stimulus-centered leftward locations. IPS1 and its putative macaque homologue, LIP, both respond selectively to the shape of visually presented objects, even when the objects are not overtly acted on (Janssen, Srivastava, Ombelet, & Orban, 2008; Konen & Kastner, 2008b; Lehky & Sereno, 2007; A. Sereno & Maunsell, 1998). The purpose of this shape selectivity has been unknown although our work (see chapters 2 and 3) suggests that it could support overt and covert orienting of attention, where the shape of an object biases the eyes and attention in a particular direction; if this bias is toward the preferred location of an LIP neuron, the neuron is more likely to preferably respond to that shape.

What at first seems inconsistent with this idea is that shape selectivity within IPS1 and LIP can be resistant to some visual transformations of the shape (Konen & Kastner, 2008b; A. Sereno & Maunsell, 1998). Given that eye position is fixed, one might expect that a shape that supposedly biased orienting toward the preferred location of a neuron would not do so anymore if translated to a different position within the picture plane. This is for the most part true if the neuron only codes for space in a retinotopic frame of reference. If some neurons, however,

primarily or additionally code for space in a stimulus-centered reference frame, then the spatial bias in that particular coordinate system should persist even though the object is moved within the picture plane. The current experiment is consistent with this possibility.

Neurons in LIP, the probable IPS1 homologue in macaques, have already been shown to transiently shift their spatial representations immediately preceding a saccade, where the neurons briefly code for the location of visual stimuli not relative to the current center of gaze, but the immediate future center of gaze (Colby & Goldberg, 1992). LIP therefore already has the available machinery to represent space relative to the center of a "virtual eye". It does not require the suspension of belief that such machinery in IPS1 could have been built upon and modified so as to maintain such a representation centered on a point in space other than the current center of gaze when the situation requires it.

Further analysis showed that IPS0 (V7), V3A, and possibly V3d also show a contralateral stimulus-centered preference where the left hemisphere tends to prefer rightward stimulus-centered locations while the right hemisphere tends to prefer leftward stimulus-centered locations. Gardner et al. (2008) measured activity in several human visual regions by independently varying fixation position and the position of target stimuli relative to the screen (although this could not be distinguished from varying locations relative to the head or other egocentric yet non-retinotopic frames of references). They reported that V3, V3A, and IPS0 all coded for spatial locations in a retinotopic reference frame. One of the possible reasons for the discrepancy between Gardner et al. (2008) and the current results is that Gardner et al. (2008) looked for the coding of locations relative to a fixed reference frame (the screen, as well as the head and trunk) while in the current study, people were asked to monitor the relative locations of two objects which both constantly changed location relative to the center of gaze, the head, the body, and the screen. The need for explicit stimulus-centered coding of space might have been much greater in the current study.

An exploratory analysis of the whole cortical surface indicated two large clusters of stimulus-centered regions within high-level visual regions. Based on the anatomical location of the more posterior cluster and its partial overlap with highly object-selective regions, we estimate this to be the location of the human MT+ complex (Dumoulin et al., 2000; Malikovic et al., 2007) and the lateral occipital complex (LOC; Malach et al., 1995). Some previous work has suggested that the LOC (McKyton & Zohary, 2007) and the human MT (d'Avossa et al., 2006)

represent locations in a spatiotopic (i.e. non-retinotopic, such as relative to the head or the borders of the screen/goggles that were used for stimulus presentation) coordinate frame while follow-up work has found spatial representations of both areas to be more consistent with the use of a pure retinotopic coordinate frame (Gardner et al., 2008; Golomb & Kanwisher, 2012). Our results are consistent with McKyton and Zohary (2007) and d'Avossa et al. (2006) but go beyond their results because these previous studies did not distinguish between a stimulus-centered reference frame and other non-retinotopic reference frames such as head-centered or body-centered. Our results indicate that the human MT+ complex can represent locations in both egocentric and stimulus-centered coordinates.

An anterior cluster showing stimulus-centered spatial coding was also found. While being mostly confined within regions that showed a preference for contralateral retinotopic space, this cluster filled in gaps in otherwise retinotopic regions. Gaps in retinotopic regions within the parietal cortex have been reported before and the reason for such dropout regions is not completely understood (Silver & Kastner, 2009; Swisher et al., 2007). We offer one possible reason, namely that these dropout regions represent space not in retinotopic coordinates but in stimulus-centered coordinates.

Given the large overlap of this anterior stimulus-centered cluster with regions that prefer contralateral retinotopic space, its general lack of object selectivity, as well as its anatomical location mostly in the superior parietal lobule but branching into the intraparietal sulcus and the postcentral sulcus (Konen & Kastner, 2008a), we judge this region to overlap with retinotopic regions IPS5 and SPL1. It has been suggested that IPS5 is homologous to the macaque area VIP (Konen & Kastner, 2008a; M. I. Sereno & Huang, 2006; Silver & Kastner, 2009) while SPL1 is homologous to the macaque parietal area 7a (Konen & Kastner, 2008a; Silver & Kastner, 2009). This is in line with recent electrophysiological work in monkeys where a population of neurons in area 7a was found to systematically vary its responses dependent on whether a task-relevant target was to the left or right of a reference object (Chafee, Averbeck, & Crowe, 2007). IPS5 and VIP can represent visual space in a head-centered coordinate system (Duhamel, Colby, & Goldberg, 1998; M. I. Sereno & Huang, 2006). Our data suggests that the human IPS5 might be capable of supporting spatial representations in other non-retinotopic coordinate systems as well, such as a stimulus-centered reference frame.

To conclude, we have shown that high-level regions of the human visual system can code for the location of an object in a stimulus-centered frame of reference. This includes regions that are part of the dorsal visual pathway, supporting the idea that the dorsal stream participates in various coordinate transformations from the native retinotopic space, not only into other egocentric coordinate systems but to reference frames centered on other objects in the world.

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CHAPTER FIVE

Summary and general discussion

In psychology and neuroscience, objects in the world and the space that they occupy are often implicitly treated as separable from each other and studied in isolation. In this thesis, I have described several experiments that explore how objects affect the space around them.

As described in chapter 2, we first recorded the activity of single neurons within the lateral intraparietal area (LIP) of the dorsal visual pathway of non-human primates. This line of research showed that rapid responses of these neurons to visual objects, responses which previously had no known function, could be directly tied to the brain region's role in the allocation of spatial attention and eye movements. The findings were two-fold. First, automatic, bottom-up neural responses to familiar visual objects reflect the organism's history of learning to associate these objects with looking toward certain spatial locations within the visual field. Secondly, fast, automatic neural responses to never-before-seen objects contain information on where a monkey will look and pay attention once these objects are encountered again in the future.

These results highlight two things from a behavioral perspective: First, with enough training, completely arbitrary associations between a visual stimulus and a behavioral response toward a spatial location can become extremely rapid and automatic. Secondly, not all associations between objects and space are made equal. There appear to be predispositions to associate objects of certain shapes with looking toward particular locations, where a completely novel object seemingly has the ability to automatically push the monkey's eyes and attention in a certain direction. This had never been previously reported.

This led to a new line of human behavioral research, described in chapter 3, which showed that objects indeed do not start out as neutral. Instead, spatial information is extracted from the shape of even completely novel, randomly generated objects. Information derived from the shape of objects is integrated into a variety of processes, such as the allocation of visual attention, the programming of eye movements, and the perception of motion. This happens swiftly and automatically without specific learning or training and is not easily overridden by experience. Up to this point, it had been a hotly debated topic whether such effects were found for highly specialized and over-learned stimuli, such as arrows and eye gaze. This work shows that effects commonly associated with such stimuli may instead represent a fundamental property of all objects.

Here, novel behavioral effects were predicted based on neurophysiological data. Had these effects not been found in people, it would have cast doubts on the generality of the neurophysiological findings. The neurophysiological and behavioral experiments complement each other, giving an example of how research in neuroscience and psychology can mutually benefit both fields.

Our interpretation of these results is that the shape of objects can directly influence weights given to different locations in a spatial priority map, thus biasing where one looks and pays attention, and that LIP can construct such a priority map. Initially, we had assumed that the map must represent space in retinotopic or eye-centered coordinates, i.e. relative to the center of gaze. There were, however, some aspects of our results and those of other people that gave hints that this might not necessarily be the case.

First of all, the results of experiment 6 in chapter 3 indicated that the shape of objects could bias attention in a particular direction regardless of the objects' starting position. This is not necessarily inconsistent with effects in a retinotopic map, such as the formation of a spatial priority gradient with low values on one side of fixation and high on the other. This nonetheless made us think about whether our effects were more easily understood as affecting priority to locations not relative to the line of sight, but relative to the objects themselves. These speculations were further bolstered by reports of both LIP and its supposed human homologues IPS1 and IPS2 showing some invariance or at least tolerance to spatial transformations of objects, such as when objects are shown from slightly different viewpoints, are translated within the picture plane, or are scaled up or down (Konen & Kastner, 2008b; A. Sereno & Maunsell, 1998).

Such reports at a first glance appear to go against our interpretations of LIP object selectivity as a manifestation of shape-derived spatial priority signals. Careful scrutiny still shows that this only needs to be the case if such transformations dramatically affect the supposed weights in the spatial priority map. My own unpublished observations show that moderate changes in an object's 3D viewpoint can still preserve the orienting behavior that it evokes. The same object seen from two moderately different viewpoints tends to evoke similar numbers of saccades of similar durations in similar directions and with saccade vectors of similar lengths. Saccadic scanpaths, just like LIP and IPS1/IPS2 object selectivity, therefore can show tolerance to changes in viewpoint.

Figure 5.1 also illustrates a hypothetical example of how a retinotopic (or eye-centered) spatial priority map could retain a degree of transformation invariance. An object can be translated (panel B), scaled up or down (panel C), and even rotated (panel D), yet still always point to the same preferred retinotopic location of a neuron.

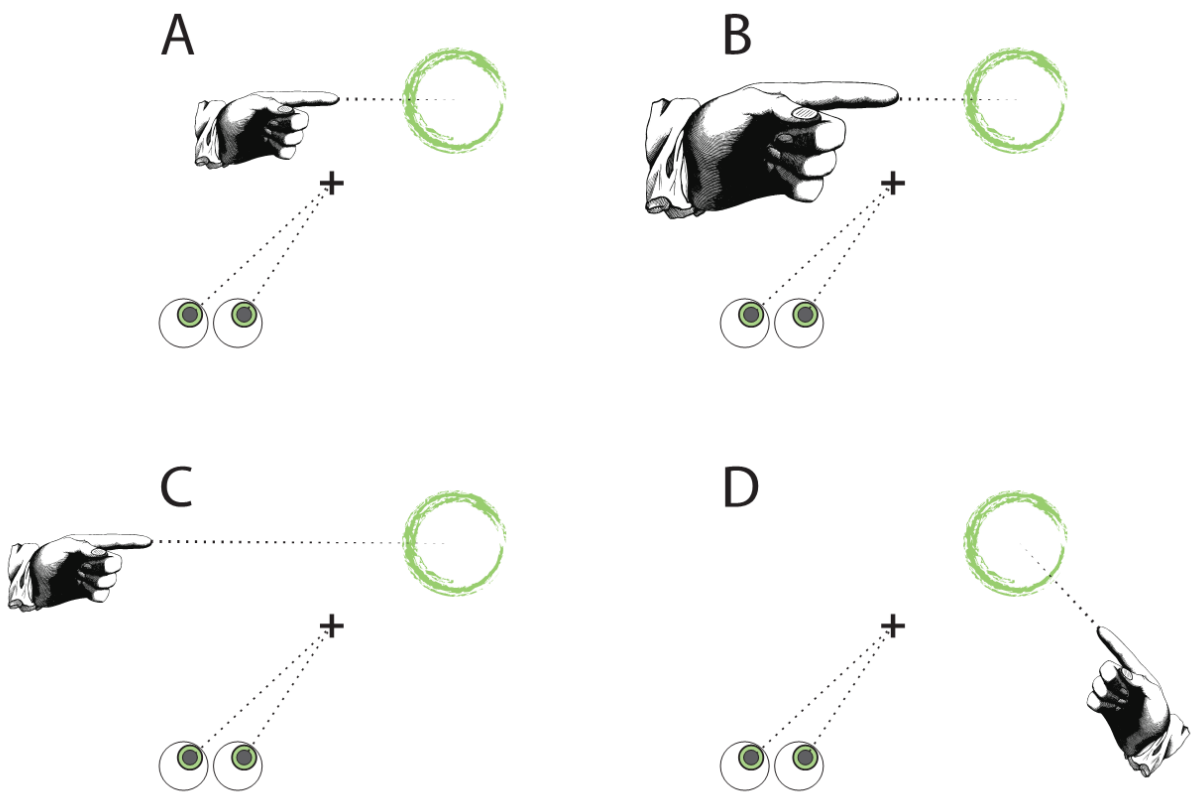

Figure 5.1. Hypothetical transformation invariance in a retinotopic spatial priority map. Even though an object goes through certain spatial transformations, it can hypothetically still point to a preferred location of a neuron despite the fact that the neuron represents space in a coordinate system centered on the line of sight. A) Before transformation. B) Scaling. C) Translation. D) Translation, mirroring, and rotation.

Some translations within the picture plane might still be problematic. As can be seen in figure 5.2, neurons that represent spatial priority in a retinotopic (or eye-centered) reference frame are not expected to tolerate certain translations of an object. If panels A and B are compared, a neuron might only be expected to become activated in panel A and not B because the object only points to its preferred retinotopic location in the former case but not the latter. If, however, the neuron in addition or instead has a preferred stimulus-centered location, as shown

in panel C, then the object still points to the same location within that reference frame and the neuron is expected to show a degree of translational invariance or tolerance.

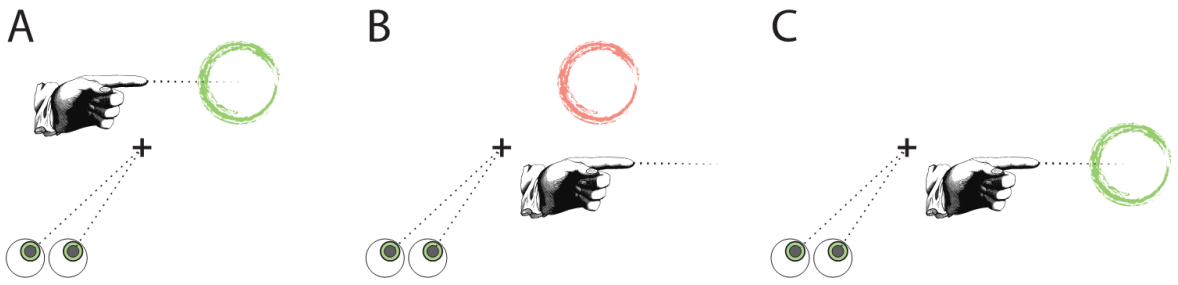

Figure 5.2. Hypothetical comparison of translational invariance and dependence in a retinotopic and stimulus-centered spatial priority map. A) Before transformation. B) After translation, the object no longer points toward a neuron's preferred retinotopic location. C) After translation, the object still point to a neuron's preferred stimulus-centered location.

As discussed in chapter 4, the human intraparietal region IPS1, a putative human homologue of LIP in the macaque, is capable of representing spatial locations in such a stimulus-centered coordinate frame in addition to a retinotopic coordinate frame. This is also true for several other high-level regions within the dorsal visual pathway. The dorsal visual pathway therefore does not only use egocentric frames of reference, but is capable of transforming visual signals from the native retinotopic space to other coordinate systems that might be more suitable to the current task or goal.

Why would a brain region that supposedly constructs a spatial priority map used for orienting guidance need to represent space in multiple reference frames? Such a complex representation of space seems unnecessary if the goal is to pick a single location in space that has the highest likelihood of containing important visual information that needs to be further scrutinized by the allocation of overt and covert visual attention.

However, we do not always just plan where we are going to look next. Saccades can be planned not as single events but as patterned sequences, where programs for saccades might be retrieved from memory in groups of more than one at a time (Zingale & Kowler, 1987). Two different modes of saccade sequence execution have been identified (Ditterich, Eggert, & Straube, 1998). In a closed-loop mode, the actor compensates for position errors during the

execution of the sequence, so the saccades are not completely preprogrammed. However, in an open-loop mode, more than one saccade vector in the sequence is preprogrammed. The saccades are executed without feedback-driven error correction so position errors propagate from one stage of the sequence to another. Ditterich et al. (1998) note that people appear to have a motor memory with a capacity for about three saccades.

When people make a saccade to target a new object, they often perform in a closed-loop mode, so that new visual information about the landing position of the previous saccade is taken into account before the new saccade vector is executed (Vergilino-Perez & Findlay, 2006). A scanning saccade within an object, however, is often coded in an open-loop mode as a fixed magnitude motor vector applied irrespective of the landing position of the preceding saccade (Vergilino-Perez & Findlay, 2006). It therefore seems like orienting behavior that is based on visual information about the shape of objects is special in the sense that it is more likely to be preprogrammed and executed without taking into account new information after a previous saccade when the eyes have moved to a new location.

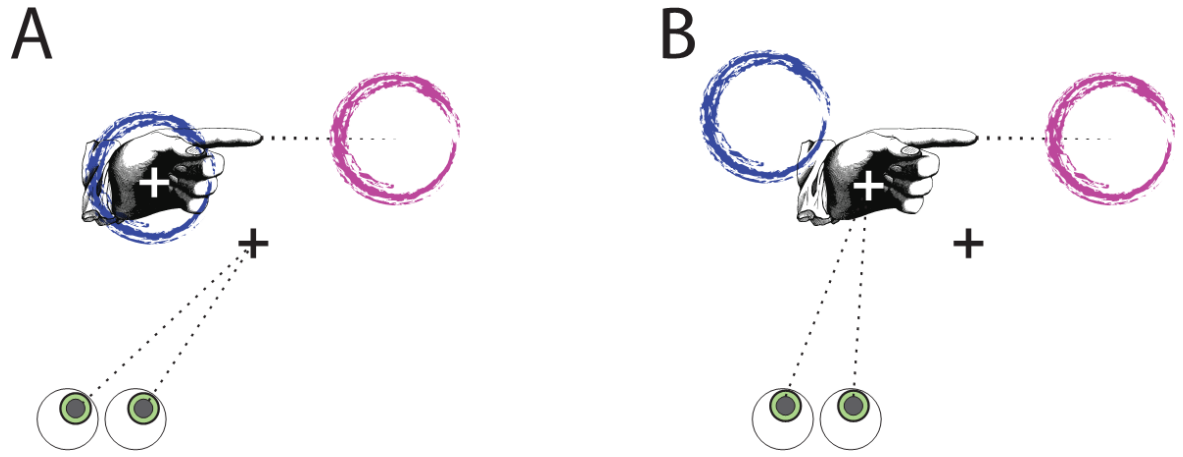

Figure 5.3. Hypothetical multi-layered priority map. An example is shown of a neuron with a preferred location both in a retinotopic coordinate system (blue) and a stimulus-centered coordinate system (pink). Such a priority map allows for the simultaneous planning of two saccades where the second saccade vector is planned relative to the location the object; this saccade vector can be executed without modification from the landing position of the first saccade on the object.

Functional studies have identified LIP and IPS1 as playing a role in visual orienting (Andersen, Snyder, Batista, Buneo, & Cohen, 2008; Andersen & Gnadt, 1989; Colby & Goldberg, 1999; Gottlieb, Kusunoki, & Goldberg, 1998; Konen & Kastner, 2008a; Mirpour, Arcizet, Ong, & Bisley, 2009). These regions also show shape selectivity and working memory related activity (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Janssen, Srivastava, Ombelet, & Orban, 2008; Konen & Kastner, 2008b; Lehky & Sereno, 2007; Mazzoni, Bracewell, Barash, & Andersen, 1996; A. Sereno & Maunsell, 1998; A. B. Sereno & Amador, 2006; Silver & Kastner, 2009; Xu & Chun, 2005). We hypothesize that LIP and IPS1 can act as a multi-orienting memory buffer. This could indicate that these regions have a multi-layered priority map. They would code for the priority of an upcoming saccade (or covert orienting of attention) to a location in a retinotopic coordinate frame, but simultaneously, they could hypothetically code for the priority of a second saccade to a location in a stimulus-centered coordinate system (see figure 5.3).

We also think that it is likely that such a multi-layered priority map is hierarchical. Let us say that there are two locations, A and B. If location A is assigned a high priority in a retinotopic map, it might be beneficial to code for the location of a second saccade vector from location A to location B so that A and B can be visited in quick succession. Location B therefore gets assigned a high priority in a map centered on location A which can be thought of as stimulus-centered coding of space. However, if one was going to compute a priority score for all points in space relative to all other points in space, the computational requirements would escalate. We therefore hypothesize that a secondary priority map is only constructed relative to one or at least few locations that have already been assigned a high priority in a primary retinotopic map. Some psychophysical evidence has already been found for the existence of the hierarchical coding of location (Baylis & Driver, 1993). We leave it to future studies to explore the neural representation of such a hierarchical priority map.

Going back to the Pioneer plaque introduced in chapter 1, would an alien race be able to decipher its message? They might not have had to hunt with bows and arrows to understand Pioneer's trajectory from Earth to Jupiter and beyond our solar system. They might, however, need to have lived in a world with a gravitational pull and atmosphere similar to that of the Earth's that would make objects move in predictable ways dependent on their shape, allowing the development of a visual system that was sensitive to such cues useful for predicting the

future from the past. In order to find their way to Earth, they might also have needed to face circumstances that required the development of complex spatial representations in multiple coordinate frames and the ability to transform such representations of space between egocentric and stimulus- or object-centered coordinate systems. So perhaps, sometime in the very distant future, we can expect a visit from intelligent extraterrestrial beings from an Earth-like environment that has molded their visual systems, through evolution and experience, to be – more or less – like ours.

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