CHAPTER 1

Naturalistic approaches to sensorimotor control

James N. Ingram* and Daniel M. Wolpert

Computational and Biological Learning Lab, Department of Engineering, University of Cambridge, Cambridge, United Kingdom

Abstract: Human sensorimotor control has been predominantly studied using fixed tasks performed under laboratory conditions. This approach has greatly advanced our understanding of the mechanisms that integrate sensory information and generate motor commands during voluntary movement. However, experimental tasks necessarily restrict the range of behaviors that are studied. Moreover, the processes studied in the laboratory may not be the same processes that subjects call upon during their everyday lives. Naturalistic approaches thus provide an important adjunct to traditional laboratory-based studies. For example, wearable self-contained tracking systems can allow subjects to be monitored outside the laboratory, where they engage spontaneously in natural everyday behavior. Similarly, advances in virtual reality technology allow laboratory-based tasks to be made more naturalistic. Here, we review naturalistic approaches, including perspectives from psychology and visual neuroscience, as well as studies and technological advances in the field of sensorimotor control.

Keywords: human sensorimotor control; natural tasks; natural behavior; movement statistics; movement kinematics; object manipulation; tool use.

Introduction

Sensorimotor control can be regarded as a series of transformations between sensory inputs and motor commands (Craig, 1989; Fogassi and Luppino, 2005; Pouget and Snyder, 2000; Rizzolatti et al., 1998; Shadmehr and Wise, 2005; Snyder, 2000; Soechting and Flanders, 1992). For example,

consider grasping an object such as a coffee cup. In order to reach for the cup, sensory information regarding its three-dimensional location, represented initially by its two-dimensional position on the retina, must be transformed into a motor command that moves the hand from its current location to the location of the cup (Shadmehr and Wise, 2005; Snyder, 2000; Soechting and Flanders, 1992). Similarly, in order to grasp the cup, sensory information regarding its three-dimensional shape must be transformed into a motor command that configures the digits to accommodate the cup

*Corresponding author.
Tel.: +44-1223-748-514; Fax: +44-1223-332-662
 E-mail: jni20@cam.ac.uk

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(Castiello, 2005; Castiello and Begliomini, 2008; Santello and Soechting, 1998). Finally, once the cup is grasped, sensory information regarding the dynamics of the cup (such as its mass) must be used to rapidly engage the transformations that will mediate control of the arm–cup combination (Atkeson and Hollerbach, 1985; Bock, 1990, 1993; Lacquaniti et al., 1982).

In many cases, the study of sensorimotor control endeavors to understand these transformations, how they are acquired and represented in the brain, how they adapt to new tasks, and how they generalize to novel task variations. When learning a new motor skill, for example, existing sensorimotor transformations may be adapted and new transformations may be learned (Haruno et al., 2001; Miall, 2002; Wolpert et al., 2001; Wolpert and Kawato, 1998). The study of motor learning can thus reveal important details about the underlying transformations (Ghahramani and Wolpert, 1997; Shadmehr, 2004). As such, many laboratory-based studies which examine sensorimotor control use adaptation paradigms in which subjects reach toward visual targets in the presence of perturbations which induce movement errors. In the case of dynamic (force) perturbations, the subject grasps the handle of a robotic manipulandum which can apply forces to the arm (see, e.g., Caithness et al., 2004; Gandolfo et al., 1996; Howard et al., 2008, 2010; Malfait et al., 2002; Shadmehr and Brashers-Krug, 1997; Shadmehr and Mussa-Ivaldi, 1994; Tcheang et al., 2007; Tong et al., 2002). Typically, the forces depend on the kinematics of the movement, such as its velocity, and cause the arm to deviate from the target. Over the course of many trials, the subject adapts to the perturbation and the deviation of the hand reduces. In the case of kinematic perturbations, the position of the subject's hand is measured and, typically, displayed as a cursor on a screen. Subjects reach toward visual targets with the cursor. A transformation (such as a rotation) can be applied to the cursor which perturbs it relative to the veridical position of the hand (see, e.g., Ghahramani and Wolpert, 1997; Ghahramani et al., 1996; Howard et al., 2010; Kagerer et al., 1997; Krakauer et al., 1999, 2000, 2005). Once again, over the course of many trials, the subject adapts to the perturbation and the deviation of the cursor reduces.

These laboratory-based perturbation studies have greatly advanced our understanding of sensorimotor control. However, because they predominantly focus on reaching movements during a limited number of perturbations, they do not capture the full range of everyday human behavior. Here, we present more naturalistic approaches. We begin by reviewing perspectives from psychology and go on to describe a naturalistic approach which has been successful in the study of the visual system. We then review studies which examine human behavior in naturalistic settings, focusing on relevant advances in technology and studies which record movement kinematics during natural everyday tasks. Because object manipulation emerges as an important component of naturalistic behavior in these studies, we finish with a review of object manipulation and tool use. Specifically, we present results from various experimental paradigms including a recent naturalistic approach in which a novel robotic manipulandum (the WristBOT) is used to simulate objects with familiar dynamics.

Naturalistic perspectives from animal psychology

The animal psychologist Nicholas Humphrey published a seminal paper in 1976 in which he speculated about the function of intelligence in primates (Humphrey, 1976). The paper begins with a conundrum: how to reconcile the remarkable cognitive abilities that many primates demonstrate in laboratory-based experiments with the apparent simplicity of their natural lives, where food is abundant (literally growing on trees), predators are few, and the only demands are to *"eat, sleep, and play."* He asked *"What—if it exists—is the natural equivalent of the laboratory*

test of intelligence?" He reasoned that if an animal could be shown to have a particular cognitive skill in the laboratory, that skill should have some natural application in the wild. He argued that the process of natural selection would not tolerate *"needless extravagance"* and that *"We do not expect to find that animals possess abilities which far exceed the calls that natural living makes upon them."* The same argument could be applied to laboratory-based studies of human sensorimotor control. For example, if we observe that subjects can adapt to a particular perturbation during a controlled laboratory-based task, what does that tell us about the sensorimotor processes that humans regularly call upon during their everyday lives? In Humphrey's case, he answered the question by carefully observing the natural behavior of primates. In the endeavor to understand the human sensorimotor system, the natural behavior of our subjects may also be an important source of information.

Whereas Humphrey encourages us to explore the natural everyday expression of the skills and processes we observe during laboratory-based tasks, other animal psychologists would argue that we should question the ecological relevance of the tasks themselves. For example, a particular primate species may fail on a laboratory-based task that is designed to characterize a specific cognitive ability (Povinelli, 2000; Povinelli and Bering, 2002; Tomasello and Call, 1997). In this case, the conclusion would be that the cognitive repertoire of the species does not include the ability in question. However, if the task is reformulated in terms of the natural everyday situations in which the animal finds itself (foraging for food, competing with conspecifics, etc.), successful performance can be unmasked (Flombaum and Santos, 2005; Hare et al., 2000, 2001). This issue of ecological relevance may also apply to the performance of human subjects during the laboratory-based tasks that are designed to study sensorimotor control (Bock and Hagemann, 2010). For example, despite our intuition that humans can successfully learn and

recall a variety of different motor skills and interact with a variety of different objects, experiments have shown that concurrent adaptation to distinct sensorimotor tasks can be difficult to achieve in the laboratory (Bock et al., 2001; Brashers-Krug et al., 1996; Goedert and Willingham, 2002; Karniel and Mussa-Ivaldi, 2002; Krakauer et al., 1999, 2005; Miall et al., 2004; Shadmehr and Brashers-Krug, 1997; Wigmore et al., 2002). However, in natural everyday life, different motor skills are often associated with distinct behavioral contexts. It is thus not surprising that when experiments are made more naturalistic by including distinct contextual cues, subjects can learn and appropriately recall laboratory-based tasks that would otherwise interfere (Howard et al., 2008, 2010; Lee and Schweighofer, 2009; Nozaki and Scott, 2009; Nozaki et al., 2006).

Naturalistic perspectives from human cognitive ethology

The importance of a naturalistic approach is also advocated by proponents of human cognitive ethology (Kingstone et al., 2008). Ethology is the study of animal (and human) behavior in natural settings (Eibl-Eibesfeldt, 1989; McFarland, 1999). The emphasis is on the adaptive and ecological significance of behavior, how it develops during the lifetime of the individual, and how it has evolved during the history of the species. It can be contrasted with the approaches of experimental psychology, which focus on laboratory-based tasks rather than natural behavior and largely ignore questions of ecological relevance and evolution (Kingstone et al., 2008). In human cognitive ethology, studies of natural real-world behavior are regarded as an important adjunct to experimental laboratory-based approaches, with some going so far as to argue that they are a necessary prerequisite (Kingstone et al., 2008). An example of this approach is given by Kingstone and colleagues and consists of a pair of studies that examine vehicle steering behavior.

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In the first study, the natural steering behavior of subjects was measured outside the laboratory in a real-world driving task (Land and Lee, 1994). In the second study, a laboratory-based driving simulator was then used to test a specific hypothesis regarding the sources of information that drivers use for steering (Land and Horwood, 1995). The experimental hypothesis was constrained by the real-world behavior of subjects, as measured in the first study, and the simulated roads were modeled on the real-world roads from which the natural dataset was collected.

Kingstone and colleagues argue that all experiments examining human cognition should begin with a characterization of the natural manifestations of the processes involved. They warn against the implicit assumption that a process identified during a controlled laboratory-based task is the same process that is naturally engaged by subjects in the real world (see also Bock and Hagemann, 2010). Learning a novel dynamic perturbation in the laboratory, for example, may be nothing like learning to use a new tool in our home workshop. If we are interesting in the sensorimotor control of object manipulation, asking subjects to grasp the handles of robots that generate novel force fields may provide only partial answers. Ideally, we should also study the natural tool-using behavior of our subjects outside the laboratory, and inside the laboratory, we should ask them to grasp a robotic manipulandum that looks and behaves like a real tool.

A naturalistic approach to the visual system

The receptive fields (RFs) of neurons in the visual system have been traditionally defined using simple artificial stimuli (for recent reviews, see Fitzpatrick, 2000; Reinagel, 2001; Ringach, 2004). For example, the circular center-surround RFs of retinal ganglion cells were originally defined using small spots of light (Hartline, 1938; Kuffler, 1953). The same method later revealed similar RFs in the lateral geniculate nucleus (Hubel, 1960; Hubel and Wiesel, 1961). In contrast, bars of light were found to elicit the largest response from neurons in primary visual cortex (V1) (Hubel and Wiesel, 1959). This finding was pivotal because it provided the first evidence for a transformation of RFs from one visual processing area to the next (Tompa and Sáry, 2010; Wurtz, 2009). A hierarchical view of visual processing emerged, in which the RFs at each level were constructed from simpler units in the preceding level (Carpenter, 2000; Gross, 2002; Gross et al., 1972; Hubel and Wiesel, 1965; Konorski, 1967; Perrett et al., 1987; Tompa and Sáry, 2010). Within this framework, using artificial stimuli to map the RFs at all stages of the visual hierarchy was regarded as essential in the effort to understand vision (Hubel and Wiesel, 1965; Tanaka, 1996; Tompa and Sáry, 2010). However, beyond their role as abstract feature detectors contributing progressively to visual perception, there was little discussion as to why RFs had particular properties (Balasubramanian and Sterling, 2009).

In contrast to traditional approaches based on artificial stimuli, the concept of efficient coding from information theory allows the properties of visual RFs to be explained in terms of natural visual stimuli (Barlow, 1961; Simoncelli, 2003; Simoncelli and Olshausen, 2001). Specifically, natural images are redundant due to correlations across both space and time (Simoncelli and Olshausen, 2001; van Hateren, 1992), and efficient coding assumes that the early stages of visual processing aim to reduce this redundancy (Barlow, 1961; van Hateren, 1992). Within such a naturalistic framework, the statistical structure of natural visual images becomes central to understanding RF properties. For example, retinal processing can be regarded as an attempt to maximize the information about the visual image that is transmitted to the brain by the optic nerve (Geisler, 2008; Laughlin, 1987). Consistent with this, center-surround RFs in the retina appear to exploit spatial correlations that exist in natural images (Balasubramanian and Sterling, 2009;

Srinivasan et al., 1982). Moreover, the RFs of both simple (Olshausen and Field, 1996) and complex (Földiak, 1991; Kording et al., 2004) cells in V1 appear to be based on an efficient neural representation of natural images. For example, simple cell RFs self-organize spontaneously under a learning algorithm that is optimized to find a sparse code for natural scenes (Olshausen and Field, 1996). Similarly, many features of complex cell RFs self-organize under a learning algorithm that is optimized to find stable responses to natural scenes (Kording et al., 2004).

Thus, whereas traditional approaches to the visual system have used artificial stimuli to simply map the structure of visual RFs, a naturalist approach based on natural visual stimuli allows the RFs to be predicted from first principles (Simoncelli and Olshausen, 2001).

Naturalistic approaches to human behavior

As reviewed in the previous section, an analysis of the natural inputs to the visual system (natural images) has been highly productive in the study of visual processing. Approaches that record the natural outputs of the sensorimotor system (everyday human behavior) may be similarly informative. Depending on the study, the data collected may include the occurrence of particular behaviors, the kinematics of movements, physical interactions with objects, social interactions with people, or the location of the subject. We briefly review studies and technologies associated with collecting behavioral data from subjects in their natural environment and then review in more detail the studies that specifically record movement kinematics during natural everyday tasks.

Studies of human behavior in naturalistic settings have traditionally relied on observation or indirect measures. Examples of the use of observation include a study of human travel behavior which required subjects to keep a 6-week travel diary (Schlich and Axhausen, 2003) and a study of the everyday use of the hand which

required an observer to keep a diary of the actions performed by subjects during the observation period (Kilbreath and Heard, 2005). In the case of indirect measures, examples include the use of e-mail logs to examine the statistics of discrete human behaviors (Barabasi, 2005), the use of dollar bill dispersal patterns to examine the statistics of human travel (Brockmann et al., 2006), and monitoring the usage of the computer mouse to examine the statistics of human movement (Slijper et al., 2009).

Recently, mobile phones have become an important tool for collecting data relevant to everyday human behavior (Eagle and Pentland, 2006, 2009). For example, large datasets of human travel patterns can be obtained from mobile phones (Anderson and Muller, 2006; González et al., 2008). In addition, mobile phones include an increasing variety of sensors, such as accelerometers, which can be used to collect data unobtrusively from naturally behaving subjects (Ganti et al., 2010; Hynes et al., 2009). This information can be used, for example, to distinguish between different everyday activities (Ganti et al., 2010). Mobile phones can also interface with small wireless sensors worn elsewhere on the body. For example, Nokia has developed a combined three-axis accelerometer and gyroscope motion sensor the size of a wristwatch which can be worn on segments of the body (Györbíró et al., 2009). This combination of accelerometers and gyroscopes has been shown to overcome the problems associated with using accelerometers alone (Luinge and Veltink, 2005; Takeda et al., 2010). The Nokia motion sensors can stream data to the subject's mobile phone via bluetooth, providing kinematic data simultaneously from multiple body segments. In a recent study, this data was used to distinguish between different everyday activities (Györbíró et al., 2009). In general, mobile phone companies are interested in determining the user's behavioral state so that the phone can respond appropriately in different contexts (Anderson and Muller, 2006; Bokharouss et al., 2007; Devlic et al., 2009;

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Ganti et al., 2010; Györbíró et al., 2009). However, the application of these technologies to naturalistic studies of human behavior is clear (Eagle and Pentland, 2006, 2009).

The interaction of subjects with objects in the environment is also an important source of information regarding naturalistic behavior (Beetz et al., 2008; Philipose et al., 2004; Tenorth et al., 2009). For example, by attaching small inexpensive radio-frequency-identification (RFID) tags to the objects in the subject's environment, a instrumented glove can be used to record the different objects used by the subject as they go about their daily routine (Beetz et al., 2008; Philipose et al., 2004). This information can be used to distinguish between different everyday tasks, and can also distinguish different stages within each task (Philipose et al., 2004). A disadvantage of the use of RFID technology is that every object must be physically tagged. An alternative method to track a subject's interactions with objects uses a head-mounted camera and image processing software to extract hand posture and the shape of the grasped object (Beetz et al., 2008).

Naturalistic studies of movement kinematics

The kinematics of a subject's movements provide an important source of information for studying sensorimotor control. However, most commercially available motion tracking systems are designed for use inside the laboratory (Kitagawa and Windor, 2008; Mündermann et al., 2006). The majority of studies which examine human movement kinematics are thus performed under laboratory conditions (for recent reviews, see Schmidt and Lee, 2005; Shadmehr and Wise, 2005). In contrast, naturalistic studies of spontaneously behaving humans require mobile, wearable systems which minimally restrict the movements of the subject. As discussed in the previous section, small wireless sensors which can stream kinematic data from multiple segments of the body to a data logger (such as a mobile phone) may provide one solution (Györbíró et al., 2009; Lee et al., 2010). However, these technologies are not yet widely available. To date, naturalistic studies of movement kinematics have thus used commercial motion tracking systems which have been modified to make them wearable by subjects. These studies, which have examined movements of the eyes, hands, and arms, are reviewed in the following sections.

Eye movements during natural tasks

Eye movements are the most frequent kind of movement that humans make, more frequent even than heartbeats (Carpenter, 2000). The oculomotor system has many features which make it an ideal model system for the study of sensorimotor control (Carpenter, 2000; Munoz, 2002; Sparks, 2002). Eye movements are relatively easy to measure (Wade and Tatler, 2005) and the neural circuitry which underlies them is well understood (Munoz, 2002; Sparks, 2002). Moreover, eye movements are intimately associated with the performance of many motor tasks (Ballard et al., 1992; Johansson et al., 2001; Land, 2009; Land and Hayhoe, 2001; Land and Tatler, 2009). They also provide a convenient behavioral marker for cognitive processes including attention (e.g., Corbetta et al., 1998) and decision making (e.g., Gold and Shadlen, 2000; Schall, 2000). It is not surprising, therefore, that a number of studies have examined eye movements during natural everyday tasks (for recent reviews, see Hayhoe and Ballard, 2005; Land, 2006, 2009; Land and Tatler, 2009).

The purpose of eye movements (saccades and smooth pursuit, for a recent review, see Krauzlis, 2005) is to move the small high-acuity spotlight of foveal vision to fixate a particular object or location in the visual scene (Land, 1999; Land and Tatler, 2009; Munoz, 2002). As such, tracking the position of the eyes during a task provides a record of what

visual information subjects are using and when they obtain it (Ballard et al., 1992; Johansson et al., 2001; Land and Hayhoe, 2001; Land and Tatler, 2009). The importance of this information during the execution of natural everyday tasks has long been recognized (reviewed in Land and Tatler, 2009; Wade and Tatler, 2005). However, early tracking systems required that the head be fixed which limited recordings to sedentary tasks performed within the laboratory (reviewed in Land and Tatler, 2009). These tasks included reading (Buswell, 1920), typing (Butsch, 1932), viewing pictures (Buswell, 1935; Yarbus, 1967), and playing the piano (Weaver, 1943).

More recently, light-weight head-free eye trackers have become available (Wade and Tatler, 2005) allowing the development of wearable, self-contained systems (Fig. 1a; Hayhoe and Ballard, 2005; Land and Tatler, 2009; Pelz and Canosa, 2001). Typically, these systems include a camera which records the visual scene as viewed by the subject along with a cursor or cross-hair which indicates the point of fixation within the scene. Studies of eye movements during natural tasks have thus moved outside the laboratory where mobile, unrestricted subjects can engage in a wider range of behaviors (Hayhoe and Ballard, 2005; Land, 2006, 2009; Land and Tatler, 2009).
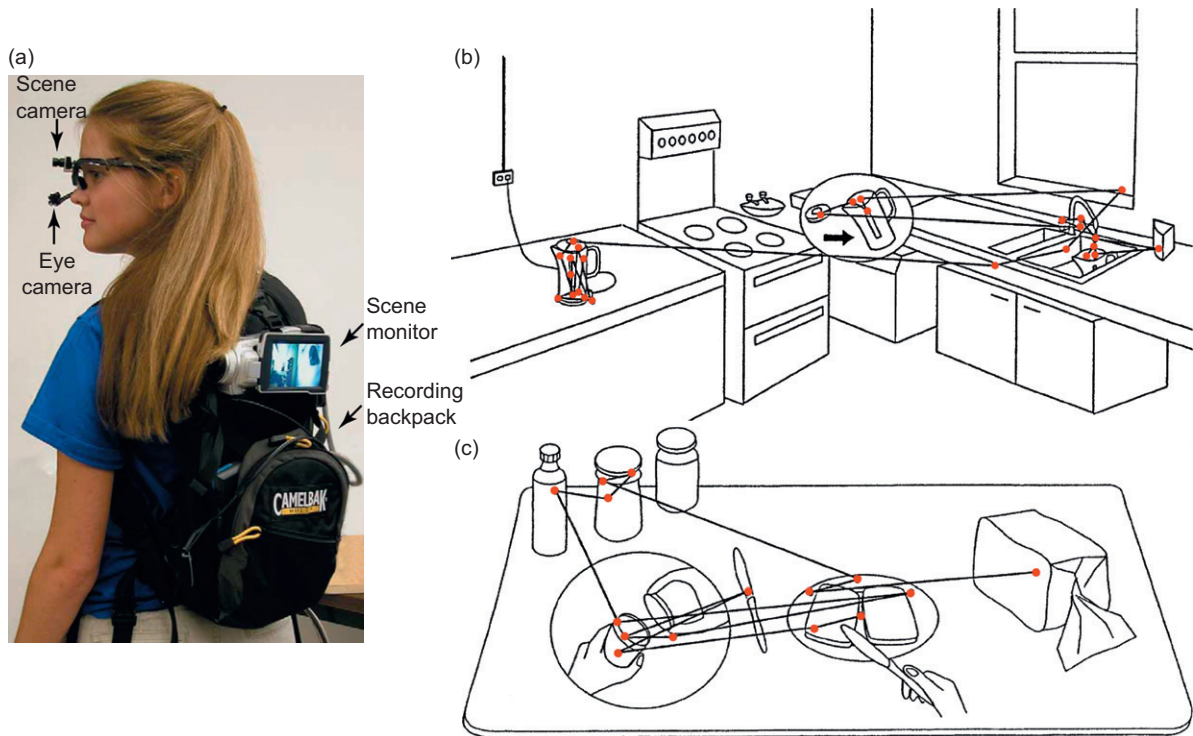

Fig. 1. Eye movements during natural tasks. Panel (a) is modified from Hayhoe and Ballard (2005). Copyright (2005), with permission from Elsevier. Panels (b) and (c) are modified from Land and Hayhoe (2001). Copyright (2001), with permission from Elsevier. (a) An example of a wearable eye-tracking system which consists of an eye camera and scene camera which are mounted on light-weight eyewear. A backpack contains the recording hardware. (b) Fixations of a typical subject while making a cup of tea. Notice the large number of fixations on objects relevant to the task (such as the electric kettle) whereas task-irrelevant objects (such as the stove) are ignored. (c) Fixations of a typical subject while making a sandwich.

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Such behaviors include everyday activities such as driving a car (Land and Lee, 1994; Land and Tatler, 2001), tea making (Fig. 1b; Land and Hayhoe, 2001; Land et al., 1999), sandwich making (Fig. 1c; Hayhoe et al., 2003; Land and Hayhoe, 2001), and hand washing (Pelz and Canosa, 2001). Ball games such as table tennis (Land and Furneaux, 1997), cricket (Land and McLeod, 2000), catch (Hayhoe et al., 2005), and squash (Land, 2009) have also been studied.

Two important findings arose from the early studies of natural eye movements during sedentary tasks. First, the pattern of eye movements is dramatically influenced by the specific requirements of the task (Yarbus, 1967), and second, eye movements usually lead movements of the arm and hand by about one second (reviewed in Land and Tatler, 2009). Contemporary laboratory-based studies have confirmed these findings by using tasks specifically designed to capture the essential features of naturalistic behavior (Ballard et al., 1992; Johansson et al., 2001; Pelz et al., 2001). One of the first studies to use this method found that, rather than relying on detailed visual memory, subjects make eye movements to gather information immediately before it is required in the task (Ballard et al., 1992). Subsequently, using the same task, it was found that subjects will even delay movements of the hand until the eye is available (Pelz et al., 2001).

Contemporary studies of eye movements during natural everyday tasks have reported similar findings. For example, when subjects make a pot of tea (Land and Hayhoe, 2001; Land et al., 1999), objects are usually fixated immediately before being used in the task, with irrelevant objects being largely ignored (Fig. 1b). A similar pattern is seen during sandwich making (Hayhoe et al., 2003; Land and Hayhoe, 2001) and hand washing (Pelz and Canosa, 2001). The influence of task requirements on eye movements is particularly striking. When subjects passively view natural scenes, they selectively fixate some areas over others based on the "bottom-up" salience of features in the scene. For example, visual attention is attracted by regions with high spatial frequencies, high edge densities or high contrast (for reviews see Henderson, 2003; Henderson and Hollingworth, 1999). In contrast, when specific tasks are imposed, the pattern of eye movements is driven by the "top-town" requirements of the task (see reviews in Ballard et al., 1992; Land and Tatler, 2009; Land, 2006). For example, while subjects are waiting for the go-signal to begin a particular task, they fixate irrelevant objects with the same frequency as the objects that are relevant to the task (Hayhoe et al., 2003). The number of irrelevant object fixations falls dramatically once the task begins.

Before studies of naturalistic eye movements, it had been assumed that subjects used visual information obtained by the eyes to construct a detailed model of the visual world which could be consulted as required during task execution (Ballard et al., 1992). The study of eye movements during natural everyday tasks outside the laboratory and during laboratory-based tasks designed to be naturalistic has shown that rather than rely on memory, subjects use their eyes to obtain information immediately before it is required in the task.

Hand and arm movements during natural tasks

The naturalistic studies of eye movements reviewed in the previous section have been made possible by the development of wearable, self-contained eye-tracking systems (Hayhoe and Ballard, 2005; Land and Tatler, 2009; Pelz and Canosa, 2001). Two recent studies from our group have used wearable, self-contained systems to record hand (Ingram et al., 2008) and arm (Howard et al., 2009a) movements during natural everyday behavior. However, in contrast to studies of eye movements, which have invariably imposed specific tasks on the subject, we allowed our subjects to engage spontaneously in natural everyday behavior.

The statistics of natural hand movements

Although the 15 joints of the hand can potentially implement 20 degrees of freedom (Jones, 1997; Stockwell, 1981), laboratory-based studies suggest that the effective dimensionality of hand movements is much less (reviewed in Jones and Lederman, 2006). For example, the ability of subjects to move the digits independently is limited (Hager-Ross and Schieber, 2000; Reilly and Hammond, 2000) due to both mechanical (Lang and Schieber, 2004; von Schroeder and Botte, 1993) and neuromuscular (Kilbreath and Gandevia, 1994; Lemon, 1997; Reilly and Schieber, 2003) factors. Moreover, the sensorimotor system is thought to employ synergies which reduce the dimensionality and thereby simplify the control problem (Mason et al., 2001; Santello et al., 1998, 2002; Schieber and Santello, 2004; Tresch et al., 2006). However, these conclusions are based on results from laboratory-based tasks which potentially constrain the variety of hand movements observed. To address this issue using a naturalistic approach, we obtained datasets of spontaneous everyday movements from the right hand of subjects who wore a self-contained motion tracking system (Ingram et al., 2008). The system consisted of an instrumented cloth glove (the commercially available CyberGlove from CyberGlove Systems) and a backpack which contained the data acquisition hardware (Fig. 2a). Subjects were fitted with the system and instructed to go about their normal daily routine. A total of 17 h of data was collected, which consisted of 19 joint angles of the digits sampled at 84 Hz.

To estimate the dimensionality of natural hand movements in the dataset, we performed a principal component analysis (PCA) on joint angular velocity (Fig. 2b and c). Consistent with the reduced dimensionality discussed above, the first 10 PCs collectively explained almost all (94%) of the variance (Fig. 2c). Moreover, the first two PCs accounted for more than half of the variance (60%) and were well conserved across subjects.

The first PC explained 40% of the variance and reflected a coordinated flexion (closing) and extension (opening) of the four fingers. The second PC explained an additional 20% of the variance and also involved flexion and extension of the four fingers. Figure 2b shows how these first two PCs combine to produce a large range of hand postures.

An important question arising from the current study is whether there are differences between the statistics of hand movements made during laboratory-based tasks and those made during everyday life. Previous studies have performed PCA on angular position data collected during a reach-to-grasp task (Santello et al., 1998, 2002). In these previous studies, the first two PCs involved flexion and extension of the fingers and accounted for 74% of the variance. When the same analysis was repeated on our dataset, the first two PCs also involved finger flexion/extension and accounted for 70% of the variance. This similarity with previous laboratory-based studies suggests that reach-to-grasp movements and object manipulation form an important component of the natural everyday tasks performed by the hand. Consistent with this, 60% of the natural use of the hands involves grasping and manipulating objects (Kilbreath and Heard, 2005).

Many previous laboratory-based studies have examined the independence of digit movements, showing that the thumb and index finger are moved relatively independently, whereas the middle and ring fingers tend to move together with the other digits (Hager-Ross and Schieber, 2000; Kilbreath and Gandevia, 1994). We quantified digit independence in our natural dataset by determining the degree to which the movements of each digit (the angular velocities of the associated joints) could be linearly predicted from the movements (angular velocities) of the remaining four digits. This measure was expressed as the percentage of unexplained variance (Fig. 2d) and was largest for the thumb, followed by the index finger, then the little and middle fingers, and was smallest for the ring
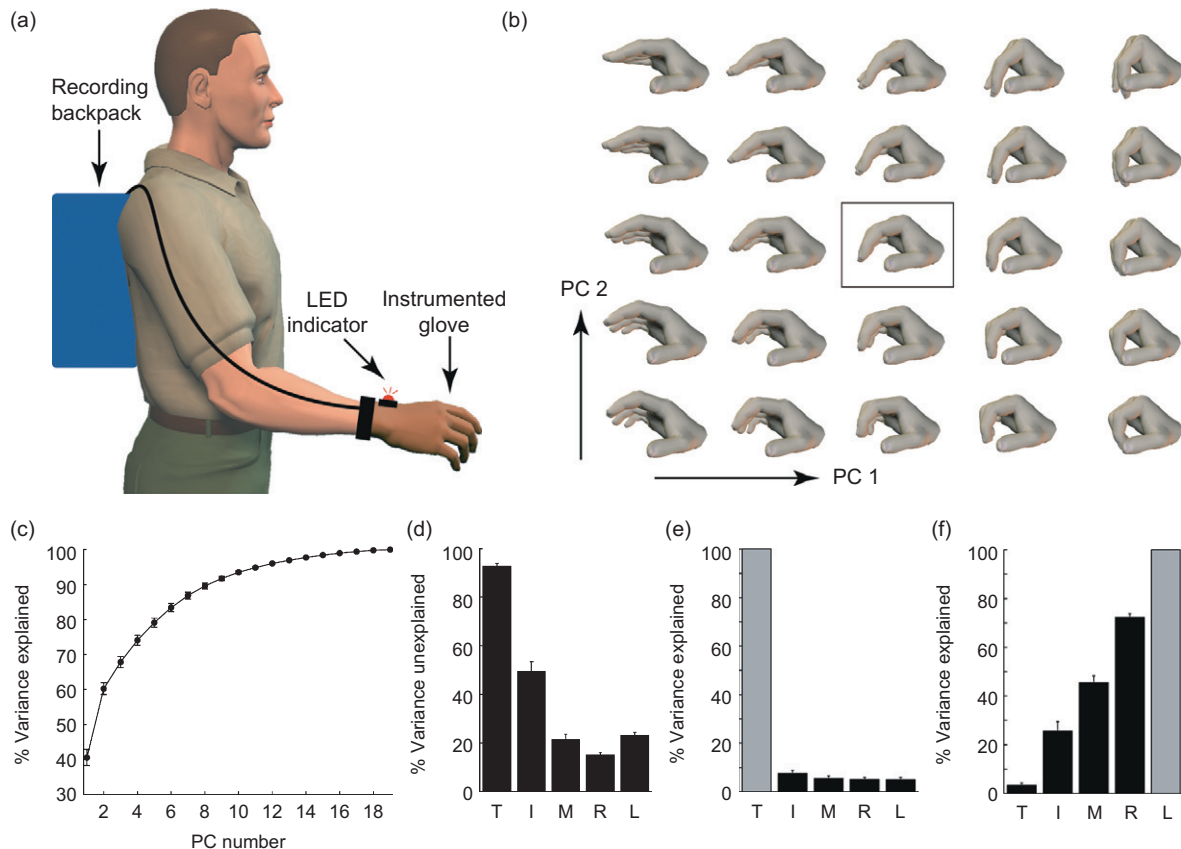
Fig. 2. The statistics of natural hand movements. Panels (b) through (f) are reprinted from Ingram et al. (2008). Used with permission. (a) The wearable motion tracking system consisted of an instrument cloth glove (the CyberGlove from CyberGlove Systems) which measured 19 joint angles of the digits. A backpack contained the recording hardware. Subjects were told to go about their normal daily routine and return when the LED indicator stopped flashing. (b) The first two principal components (PC) explained 60% of the variance in joint angular velocity and combine to produce a range of hand postures. (c) The percent variance explained by increasing numbers of principal components. The first 10 PCs accounted for 94% of the variance in joint angular velocity. (d) The percent variance in angular velocity which remained unexplained for each digit after a linear reconstruction which was based on data from the other four digits (T=Thumb, I=Index, M=Middle, R=Ring, L=Little). (e) The percent variance in angular velocity which was explained by a linear reconstruction which paired the thumb individually with the other digits. The gray 100% bar indicated self-pairing. (f) The percent variance explained for digit pairs involving the little finger, plotted as in (e).

finger. Interestingly, this pattern of digit independence was correlated with results from several previous studies, including the number of cortical sites encoding movement of each digit (Penfield and Broldrey, 1937) and a laboratory-based measure of the ability of subjects to move each digit individually (Hager-Ross and Schieber, 2000).

We also quantified coupling between pairs of digits, applying the linear reconstruction method separately to each digit paired separately with the other four digits. This measure was expressed as the percent variance that was explained. Results for the thumb (Fig. 2e) show that its movements are very difficult to predict based on

movements of the fingers. Results for the fingers show that the best linear reconstructions (highest coupling) are based on the movements of the immediately neighboring fingers, decreasing progressively with increasing distance (Fig. 2f shows this pattern for the little finger). Thus, whereas the thumb moves independently of the fingers, the movements of a given finger are more or less related to neighboring fingers based on the topological distance between them.

These results from a naturalistic study of hand movements have generally supported those obtained from previous laboratory-based studies. However, because previous studies have employed a limited number of experimental tasks, it is important to verify their conclusions in the natural everyday behavior of subjects. Specifically, we have verified the pattern of digit independence in the everyday use of the hand and shown that many aspects of natural hand movements have been well characterized by laboratory-based studies in which subjects reach to grasp objects.

The statistics of natural arm movements

Many laboratory-based studies have examined the ability of subjects to make bimanual movements with particular phase relations (Kelso, 1984, 1995; Li et al., 2005; Mechsner et al., 2001; Schmidt et al., 1993; Swinnen et al., 1998, 2002). Results indicate that not all phase relations are equally easy to perform. At a low frequency of movement, both symmetric movements (phase difference between the two arms of 0°) and antisymmetric movements (phase difference of 180°) are easy to perform, whereas movements with intermediate phase relations are more difficult. At higher frequencies, only symmetric movements can be performed easily and all other phase relations tend to transition to the symmetric mode (Tuller and Kelso, 1989; Wimmers et al., 1992). This "symmetry bias" has been extensively studied in laboratory-based

experiments and there has been much debate regarding its significance and underlying substrate (e.g., Mechsner et al., 2001; Treffner and Turvey, 1996). Its relevance to the everyday behavior of subjects, however, is not clear. To address this issue using a naturalistic approach, we obtained datasets of spontaneous everyday arm movements of subjects who wore a self-contained motion tracking system (Howard et al., 2009a). We hypothesized that the symmetry bias would be reflected in the natural statistics of everyday tasks. Electromagnetic sensors (the commercially available Liberty system from Polhemus) were attached to the left and right arms and the data acquisition hardware was contained in a backpack (Fig. 3a). Subjects were fitted with the system and instructed to go about their normal routine. A total of 31 h of data was collected, which consisted of the position and orientation of the sensors on the upper and lower segments of the left and right arms sampled at 120 Hz.

We analyzed the phase relations between flexion/extension movements of the right and left elbow, calculating the natural incidence of different phase relations for a range of movement frequencies (Fig. 3b and c). At low movement frequencies, the distribution of phase incidence was bimodal with peaks for both symmetric and antisymmetric movements (see also Fig. 3d). At higher movement frequencies, phase incidence became unimodal and was dominated by symmetric movements. The progression of phase incidence from a bimodal to a unimodal distribution as movement frequency increases can be seen in Fig. 3b. These results provide an important adjunct to laboratory-based studies because they show that the symmetry bias is expressed in the natural everyday movements of subjects.

The coordinate system in which the symmetry bias is expressed is an important issue which has been examined in laboratory-based studies (Mechsner et al., 2001; Swinnen et al., 1998). If the symmetry bias is expressed only in joint-based (intrinsic) coordinates (Fig. 3c), it may be a property of sensorimotor control or the
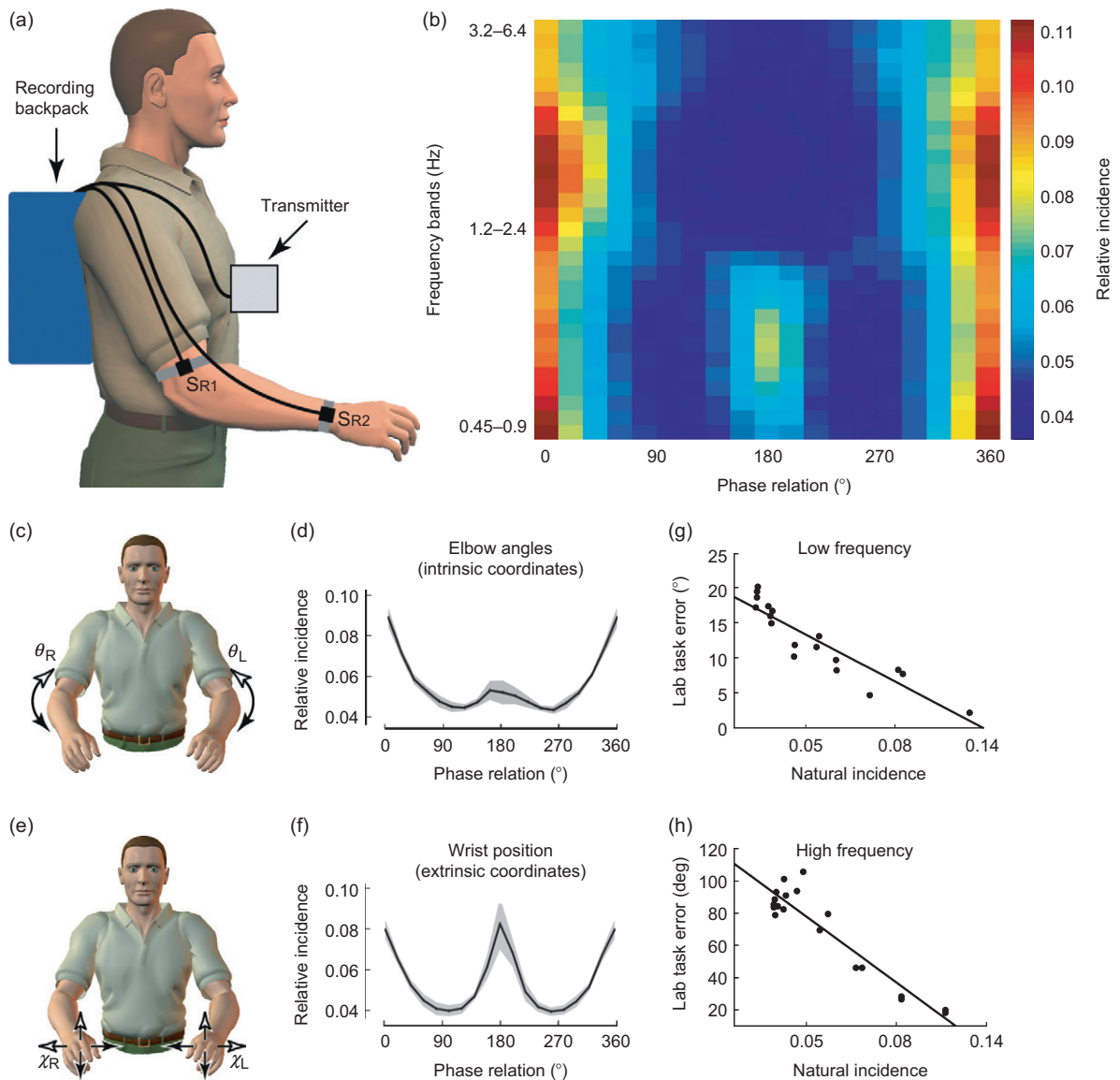
Fig. 3. The statistics of natural arm movements. Panels (b) through (h) are reprinted from Howard et al. (2009a). Used with permission. (a) The wearable motion tracking system consisted of small electromagnetic sensors and a transmitter (the Liberty system from Polhemus). A backpack contained the recording hardware. The sensors were attached to the upper and lower segments of the left and right arms as shown (S_{R1}=right upper, S_{R2}=right lower; left arm and sensors not shown). (b) Distributions of relative phases between left and right elbow joint angles. Note bimodal distribution at low movement frequencies consisting of both symmetric (0°/360°) and antisymmetric (180°) phases and unimodal distribution at higher frequencies consisting of symmetric phase only. (c) Elbow angles represent an intrinsic coordinate system for representing movements of the arms. Symmetric movements are shown by homogenous left/right pairings of arrow heads (left filled with right filled or left open with right open). Antisymmetric movements are shown by heterogeneous left/right pairings of arrow heads (left filled with right open or right open with left filled). (d) Relative incidence of different phase relations at low frequencies for natural movements represented in intrinsic coordinates (as shown in (c)). (e) Wrist positions in Cartesian coordinates represent an extrinsic coordinate system for representing movements of the arms. Symmetric and antisymmetric movements are shown as in (c). (f) Relative incidence of different phase relations at low frequencies for natural movements represented in extrinsic coordinates (as shown in (e)). (g) Error during the low frequency laboratory-based tracking task for different phase relations plotted against log of the natural incidence of those phase relations. (h) Error during the high-frequency laboratory-based tracking task for different phase relations plotted against log of the natural incidence of those phase relations.

musculoskeletal system. However, if the symmetry bias is expressed in external (extrinsic) coordinates (Fig. 3e), it may be a property of the naturalistic tasks which humans regularly perform. For example, bimanual object manipulation is frequent during everyday life (Kilbreath and Heard, 2005) and imposes particular constraints on movements expressed in extrinsic coordinates (Howard et al., 2009a). Specifically, moving the hands together (or apart) to bimanually grasp (or release) an object requires antisymmetric movements, whereas transporting an object once it is grasped requires symmetric movements. If the constraints of bimanual object manipulation are important, then the symmetry bias should be more pronounced for movements expressed in extrinsic coordinates (relevant to the object). To examine this issue, we compared the phase incidence of natural movements defined in intrinsic space (elbow joint angle; Fig. 3c and d) with those defined in extrinsic space (the Cartesian position of sensors on the wrist; Fig. 3e and f). The distribution of phase incidence was bimodal in both cases. However, the incidence of 180° phase was much higher for the movements defined in extrinsic space, occurring as frequently in this case as symmetric movements. This suggests that natural everyday tasks are biased toward both symmetric and antisymmetric movements of the hands in extrinsic space, consistent with the constraints of bimanual object manipulation.

An interesting question concerns the relationship between the level of performance on a particular task and the frequency with which that task is performed. It is well known that training improves performance, but with diminishing returns as the length of training increases (Newell and Rosenbloom, 1981). Specifically, relative performance is often related to the log of the number of training trials. This logarithmic dependence applies to a wide range of cognitive tasks including multiplication, visual search, sequence learning, rule learning, and mental rotation (Heathcote et al., 2000). We examined this issue by comparing the incidence of movement phases in

the natural movement dataset with performance on a laboratory-based bimanual tracking task. Subjects tracked two targets (one with each hand) which moved sinusoidally with various phase relations during a low- and high-frequency condition. The performance error on the task was negatively correlated with the log of the phase incidence of natural movements at both low (Fig. 3g) and high (Fig. 3h) frequencies. This demonstrates that the logarithmic training law holds between the natural incidence of everyday movements and performance on a laboratory-based task.

Naturalistic approaches to object manipulation

In previous sections, object manipulation emerged as a key feature of naturalistic human behavior. For example, during everyday life, humans spend over half their time (60%) grasping and manipulating objects (Kilbreath and Heard, 2005). Not surprisingly, the statistics of natural hand (Ingram et al., 2008) and arm (Howard et al., 2009a) movements are also consistent with grasping and manipulating objects. Moreover, eye movements during natural tasks are dominated by interactions with objects (Land and Tatler, 2009). Studies which examine object manipulation should thus form an important component of naturalistic approaches to human sensorimotor control.

An ethology of human object manipulation

The ability to manipulate objects and use them as tools constitutes a central theme in the study of human biology. For example, the sensorimotor development of human infants is divided into stages which are characterized by an increasing repertoire of object manipulation and tool-using skills (Case, 1985; Parker and Gibson, 1977; Piaget, 1954). Infants begin with simple prehension and manipulation of objects between

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4–8 months and finally progress to the insightful use of objects as tools by 12–18 months. This first evidence for tool use is regarded as a milestone in human development (Case, 1985; Piaget, 1954). Similarly, the first evidence for tool use in the archeological record (2.5 million years ago) is regarded as a milestone in human evolution (Ambrose, 2001; Parker, 1974). The long evolutionary history of tool use by humans and their ancestors is thought to have influenced the dexterity of the hand (Marzke, 1992; Napier, 1980; Tocheri et al., 2008; Wilson, 1998) and the size and complexity of the brain (Ambrose, 2001; Wilson, 1998). Indeed, the oldest stone tools, although simple, required significant sensorimotor skill to use and manufacture (Pelegrin, 2005; Roche et al., 1999; Schick et al., 1999; Stout and Semaw, 2006; Toth et al., 1993). Object manipulation and tool use is also an important diagnostic feature for comparative studies of animal behavior, especially those comparing the sensorimotor and cognitive skills of humans with other primates (Parker and Gibson, 1977; Torigoe, 1985; Vauclair, 1982, 1984; Vauclair and Bard, 1983). It is known, for example, that a number of animals regularly use and even manufacture tools in their natural environments (Anderson, 2002; Brosnan, 2009; Goodall, 1963, 1968). However, the human ability and propensity for tool use far exceeds that observed in other animals (Boesch and Boesch, 1993; Povinelli, 2000; Schick et al., 1999; Toth et al., 1993; Vauclair, 1984; Visalberghi, 1993).

Object manipulation is mediated by a number of interacting processes in the brain including visual object recognition (Wallis and Bulthoff, 1999), retrieval of semantic and functional information about the object (Johnson-Frey, 2004), encoding object shape for effective grasping (Castiello, 2005; Castiello and Begliomini, 2008; Santello and Soechting, 1998), and incorporating the object into the somatosensory representation of the body (Cardinali et al., 2009; Maravita and Iriki, 2004). Object manipulation also represents a challenge for sensorimotor control because

grasping an object can dramatically change the dynamics of the arm (Atkeson and Hollerbach, 1985; Bock, 1990; Lacquaniti et al., 1982). Thus, to continue moving skillfully after grasping an object, the motor commands must adapt to the particular dynamics of the object (Atkeson and Hollerbach, 1985; Bock, 1990, 1993; Johansson, 1998; Lacquaniti et al., 1982). This process is thought to be mediated by internal models of object dynamics (Flanagan et al., 2006; Wolpert and Flanagan, 2001), and a great deal of research has been devoted to understanding how internal models are acquired and represented and how they contribute to skillful object manipulation. This research has employed three main experimental approaches which are reviewed in the following sections. The first approach involves tasks in which subjects manipulate real physical objects. The remaining two approaches involve the use of robotic manipulanda to simulate virtual objects. As described below, the use of virtual objects removes the constraints associated with physical objects because the dynamics and visual feedback are under computer control.

Physical objects with familiar dynamics

Laboratory-based experiments in which subjects interact with physical objects that have familiar dynamics allow the representations and skills associated with everyday object manipulation to be examined. As reviewed previously, the ability to perform skilled movements while grasping an object requires the rapid adaptation of the motor commands that control the arm to account for the dynamics associated with the grasped object. The efficacy of this process can be observed in the first movement subjects make immediately after grasping a heavy object. If the mass of the object is known, the kinematics of the first movement made with the object are essentially identical to previous movements made without it (Atkeson and Hollerbach, 1985; Lacquaniti et al., 1982). If the mass is unknown, subjects adapt rapidly

before the first movement is finished (Bock, 1990, 1993). Rapid adaptation is also observed when subjects grasp an object in order to lift it (reviewed in Johansson, 1998). In this case, subjects adapt both the forces applied by the digits to grasp the object (the grip force) and the forces applied by the arm to lift it. When lifting an object that is heavier or lighter than expected, for example, subjects adapt their grip force to the actual mass within just a few trials (Flanagan and Beltzner, 2000; Gordon et al., 1993; Johansson and Westling, 1988; Nowak et al., 2007). Subjects also use visual and haptic cues about the size of the object to estimate the grip force applied during lifting (Gordon et al., 1991a,b,c). For familiar everyday objects, subjects can generate appropriate forces on the very first trial (Gordon et al., 1993). Rapid adaptation is also observed when subjects lift a visually symmetric object which has an asymmetrically offset center of mass (Fu et al., 2010; Salimi et al., 2000; Zhang et al., 2010). In this case, subjects predictively generate a compensatory torque at the digits to prevent the object from tilting, a response which develops within the first few trials (Fu et al., 2010).

This ability of subjects to rapidly adapt when grasping an object suggests that the sensorimotor system represents the dynamics of objects. Further evidence that subjects have knowledge of object dynamics comes from experiments which examine the perceptual abilities referred to as dynamic touch. Dynamic touch is the ability to perceive the properties of an object based on the forces and torques experienced during manipulation (Gibson, 1966; Turvey, 1996). In a typical experiment, subjects are required to perceive a particular object property after manipulating it behind a screen which occludes vision (reviewed in Turvey, 1996). For example, subjects can use dynamic touch to perceive both the length of a cylindrical rod (Solomon and Turvey, 1988) and the position along the rod at which they grasp it (Pagano et al., 1994). If the rod has a right-angle segment attached to its distal end (to make an elongated "L" shape), subjects can perceive the orientation of the end segment (Pagano and Turvey, 1992; Turvey et al., 1992). These abilities suggest that subjects extract information from the relationship between the movements they make with an object (the kinematics) and the associated forces and torques. By combining information from dynamic touch with visual information, the perception of object properties can be made more precise (Ernst and Banks, 2002). Thus, both dynamic touch and vision are likely to contribute during naturalistic object manipulation.

Simulated objects with unfamiliar dynamics

The range of experimental manipulations available during tasks that use physical objects is limited. The dynamics are constrained to rigid body physics and the precise control of visual feedback is difficult. An extensively used approach which addresses these limitations uses robot manipulanda to simulate novel dynamics combined with display systems to present computer-controlled visual feedback (see reviews in Howard et al., 2009b; Wolpert and Flanagan, 2010). In these experiments, the subject is seated and grasps the handle of a robotic manipulandum which can apply state-dependent forces to the hand. In many of these experiments, the forces depend on the velocity of the hand and are rotated to be perpendicular to the direction of movement (Caithness et al., 2004; Gandolfo et al., 1996; Howard et al., 2008, 2010; Malfait et al., 2002; Shadmehr and Brashers-Krug, 1997; Shadmehr and Mussa-Ivaldi, 1994; Tcheang et al., 2007; Tong et al., 2002). Visual targets are presented using the display system and subjects make reaching movements to the targets from a central starting position. In the initial "null" condition, the motors of the robot are turned off. In this case, subjects have no difficulty reaching the targets and make movements which are approximately straight lines. When the force field is turned on, movement paths are initially perturbed in the direction of the field. Over many trials, the

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movements progressively return to their original kinematic form as subjects adapt to the perturbing dynamics. This progressive adaptation can be shown to be associated with the acquisition of an internal model of the dynamics. If the force field is unexpectedly turned off, for example, movement paths are perturbed in the opposite direction. This is because subjects generate the forces they expect, based on their acquired internal model of the perturbing dynamics.

Dynamic perturbation studies have provided detailed information about the processes of sensorimotor adaptation and the associated representations of dynamics. However, the applicability of the results to everyday object manipulation is not clear (Lackner and DiZio, 2005). In some respects, the learned dynamics appear to be associated with an internal model of a grasped object (Cothros et al., 2006, 2009). In other respects, the learned dynamics appear to be associated with an internal model of the arm (Karniel and Mussa-Ivaldi, 2002; Malfait et al., 2002; Shadmehr and Mussa-Ivaldi, 1994). Moreover, the majority of studies have examined adaptation to novel dynamics, which occurs over tens or hundreds of trials. In contrast, as reviewed in the previous section, humans adapt to the familiar dynamics of objects they encounter during everyday life within just a few trials. In addition, the robotic devices used in most studies generate only translational forces that depend only on the translational kinematics of the hand. In contrast, naturalistic objects generate both translational forces and rotational torques that depend on the translational and rotational kinematics of the object (as well as its orientation in external space). In the next section, an approach which addresses these issues is presented.

Simulated objects with familiar dynamics

Robot manipulanda can be used to simulate objects with familiar dynamics (see review in Wolpert and Flanagan, 2010), thereby combining aspects from the two approaches reviewed above. This allows the processes associated with naturalistic object manipulation to be examined, without the constraints imposed by the physics of real-world objects. However, only a relatively small number of studies have used this approach. For example, the coordination of grip force has been examined during bimanual manipulation of a simulated object. In this case, the dynamics could be coupled or uncoupled between the left and right hands, allowing the effect of object linkage to be examined (White et al., 2008; Witney and Wolpert, 2003; Witney et al., 2000). When the dynamics were coupled, the object behaved like a single object that was grasped between the two hands (see also Howard et al., 2008). Grip force modulation has also been examined using a simulated object which is grasped between the thumb and index finger (Mawase and Karniel, 2010). In this case, the study replicated the object lifting task used in the many grip force studies reviewed above, but with the greater potential for experimental control offered by a simulated environment.

Recently, we have taken a different approach by developing a novel planar robotic manipulandum (the WristBOT; Fig. 4a) which includes rotational torque control at the vertical handle (Howard et al., 2009b). Combined with a virtual reality display system, this allows us to simulate the dynamics and visual feedback of an object which can be rotated and translated in the horizontal plane (Howard et al., 2009b; Ingram et al., 2010). The object resembles a small hammer (Fig. 4b), and consists of a mass on the end of a rigid rod. Subjects manipulate the object by grasping the handle at the base of the rod (Fig. 4b). Rotating the object generates both a torque and a force. The torque depends on the angular acceleration of the object. The force can be derived from two orthogonal components. The first and major component (the tangential force) is due to the tangential acceleration of the mass and is always perpendicular to the rod. The second and minor component (the
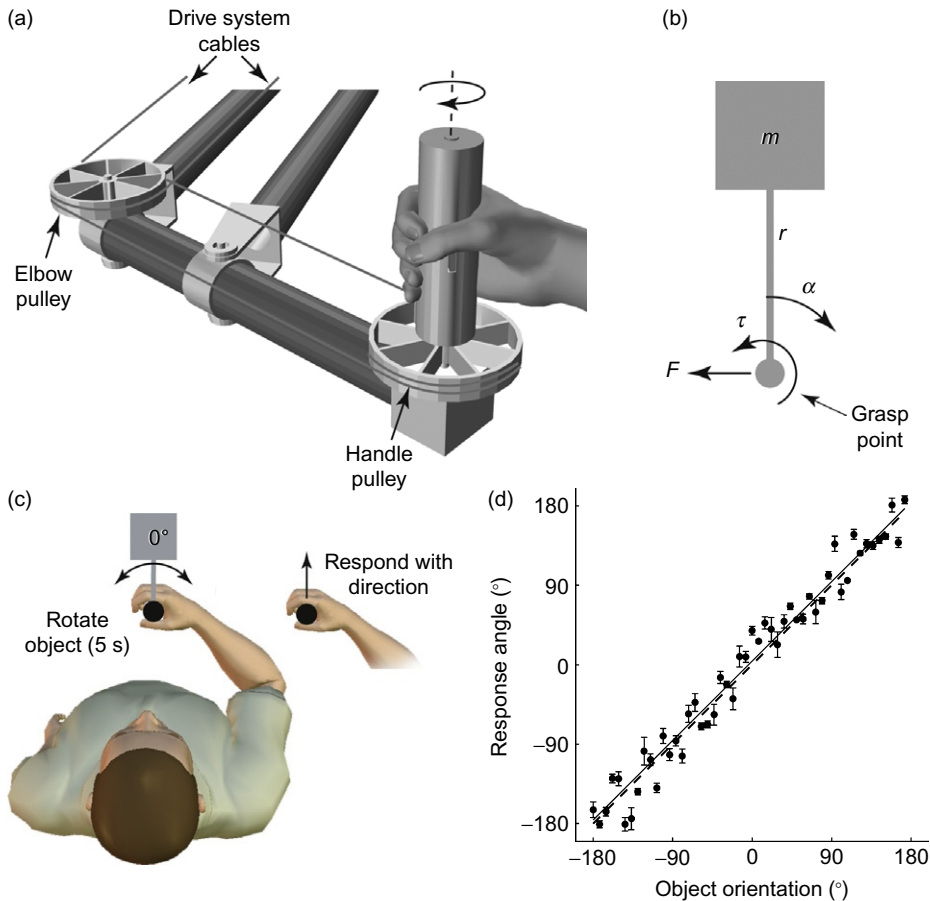
Fig. 4. The WristBOT robotic manipulandum, simulated object, and haptic discrimination task. Panel (a) is reprinted from Ingram et al. (2010). Copyright (2010), with permission from Elsevier. Panels (b) through (d) are reprinted from Howard et al. (2009b). Copyright (2009), with permission from Elsevier. (a) The WristBOT is a modified version of the vBOT planar two-dimensional robotic manipulandum. It includes an additional degree of freedom allowing torque control around the vertical handle. Cables and pulleys (only two of which are shown) implement the transmission system between the handle and the drive system at the rear of the manipulandum (not shown). (b) The dynamics of the virtual object were simulated as a point mass (mass m) on the end of a rigid rod (length r) of zero mass. Subjects grasped the object at the base of the rod. When rotated clockwise (as shown), the object generated a counter-clockwise torque (τ) due to the angular acceleration (α) of the object. The object also generated a force (F) due to the circular motion of the mass. At the peak angular acceleration, the force was perpendicular to the rod, as shown. Importantly, the orientation of the force changes with the orientation of the object. (c) The haptic discrimination task required subjects to rotate the object for 5 s and then make a movement toward the perceived direction of the mass. The object was presented at a different orientation on every trial. Visual feedback was withheld. (d) Response angle (circular mean and circular standard error) across subjects plotted against actual orientation of the object. Solid line shows circular linear fit to subject responses and dashed line shows perfect performance.

centripetal force) is due to the circular velocity of the mass and acts along the rod toward the center of rotation. Simulations demonstrated that the

peak force acts in a direction that is close to perpendicular to the rod. Thus, as subjects rotate the object, the force experienced at the handle

will perturb the hand in a direction that depends on the orientation of the object. In the following sections, we review two recent studies which have used this simulated object.

Haptic discrimination task

The direction of the forces associated with rotating an object provides a potential source of information regarding its orientation (or rather, the orientation of its center of mass). Previous studies of haptic perception have used physical objects and have suggested that subjects use torque to determine the orientation of the principal axis of the object (Pagano and Turvey, 1992; Turvey, 1996; Turvey et al., 1992). Specifically, the smallest torque is associated with rotating the object around its principal axis. We used a simulated haptic discrimination task (Fig. 4c) to determine if subjects can also use force direction to perceive object orientation (Howard et al., 2009b). In the case of our simulated object, force direction was the only source of information because torque is independent of orientation when rotating around a fixed axis. Subjects first rotated the simulated object back and forth for 5 s in the absence of visual feedback and then indicated the orientation of the object by making a movement toward the perceived location of the center of mass. Results showed that subjects could accurately perceive the orientation of the object based on its simulated dynamics (Fig. 4d). This suggests that the forces associated with rotating an object are an important source of information regarding object orientation.

Object manipulation task

To examine the representation of dynamics associated with familiar everyday objects, we developed a manipulation task that required subjects to rotate the simulated object while keeping its handle stationary (Ingram et al.,

2010). The visual orientation and dynamics of the object could be varied from trial to trial (Fig. 5a). To successfully perform the task, subjects had to generate a torque to rotate the object as well as a force to keep the handle stationary. As described above, the direction of the force depends on the orientation of the object (see Fig. 4b). In the first experiment, the object was presented at different visual orientations (see inset of Fig. 5a). Subjects experienced the torque as they rotated the object, but not the forces. Instead, the manipulandum simulated a stiff spring which clamped the handle in place. This allowed us to measure the anticipatory forces produced by subjects in the absence of the forces normally produced by the object. Results showed that subjects produce anticipatory forces in directions that were appropriate for the visual orientation of the object (Fig. 5b). That is, subjects produce forces that are directed to oppose the forces they expect the object to produce. Importantly, subjects do this before they have experienced the full dynamics of the object, providing evidence that they have a preexisting representation of the dynamics that can be recalled based on visual information. In subsequent experiments, we examined the structure of this representation, how it adapted when exposed to the dynamics of a particular object, and how it was modulated by the visual orientation of the object.

In a second experiment, we examined the time course of adaptation (Fig. 5c). Subjects first experienced the object with the forces normally generated by its dynamics turned off. After they had adapted to this zero-force object (pre-exposure phase in Fig. 5c), the forces were unexpectedly turned on. Although this caused large deviations of the handle on the first few trials, these errors rapidly decreased over subsequent trials as subjects adapted the magnitude of their forces to stabilize the object (exposure phase in Fig. 5c). After many trials of exposure to the normal dynamics of the object, the forces associated with rotating the object were again turned off (postexposure phase in
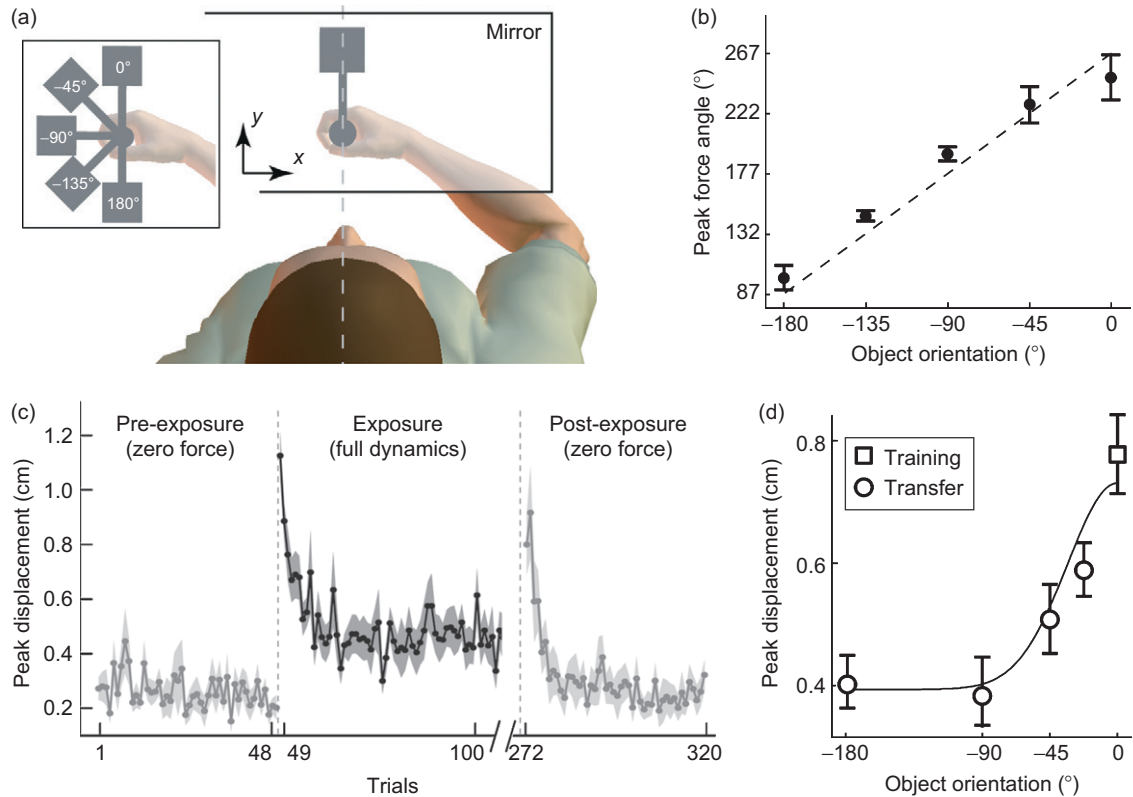
Fig. 5. The representation of familiar object dynamics. Panel (a) (modified) and panels (b) and (d) (reprinted) are from Ingram et al. (2010). Copyright (2010), with permission from Elsevier. (a) Top view of subject showing visual feedback of the object projected over the hand. The mirror prevents subject from seeing either their hand or the manipulandum. Dashed line shows subject's midline. Inset shows the object presented at different visual orientations. (b) The angle of the peak force produced by subjects as they rotate the object (circular mean and circular standard error) plotted against the visual orientation of the object. The dashed line shows perfect performance. (c) Peak displacement of the handle of the object plotted against trial number. Peak displacement increases when the forces associated with rotating the object are unexpectedly turned on (exposure), decreasing rapidly over the next few trials to an asymptotic level. Peak displacement increases again when the forces are unexpectedly turned off (postexposure), decreasing rapidly to preexposure levels. (d) Peak displacement plotted against the orientation of the object. Subjects experience the full dynamics of the object at the training orientation (square) and are presented with a small number of probe trials at transfer orientations (circles) with the forces turned off. Peak displacement is a measure of the forces subjects produce as they rotate the object. The largest forces (displacements) are produced at the training orientation and decrease progressively as the orientation of the object increases relative to the training orientation. Solid line shows the mean of a Gaussian fit individually to each subject (mean standard deviation of Gaussian fit = 34°).

Fig. 5c). This initially caused large deviations of the handle, due to the large forces that subjects had learned to produce during the exposure phase. Once again, these errors rapidly decreased over subsequent trials as subjects adapted the magnitude of their forces to be appropriate for the zero-force object. Importantly, these results show that the rapid adaptation characteristic of manipulating everyday objects can also occur when subjects manipulate simulated objects, provided the dynamics are familiar (see also Witney et al., 2000).

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In a third experiment, we presented subjects with objects of three different masses to examine how this experience would influence the magnitude of the forces they produced. As expected, subjects adapted the force magnitude according to the mass of the object. Similar results have been obtained for grip force when subjects lift objects of varying mass (Flanagan and Beltzner, 2000; Gordon et al., 1993; Johansson and Westling, 1988; Nowak et al., 2007). The adaptation of force magnitude was further examined in a fourth experiment which examined generalization. Studies of generalization can reveal important details of how dynamics are represented (Shadmehr, 2004). Subjects experienced the object at a single training orientation after which force magnitude was examined at five visual orientations, including four novel orientations where the object had not been experienced. We observed a Gaussian pattern of generalization, with the largest forces produced at the training orientation, decreasing progressively as the orientation increased relative to the training orientation (Fig. 5d). Results from this experiment are consistent with multiple local representations of object dynamics because a single general representation would predict perfect generalization.

In summary, using a novel robotic manipulation to simulate a familiar naturalistic object, we have shown that subjects have a preexisting representation of the associated dynamics. Subjects can recall this representation based on vision of the object and can use it for haptic perception when visual information is not available. During manipulation, adaptation of the representation to a particular object is rapid, consistent with many previous studies in which subjects manipulate physical objects. Adaptation is also context specific, being locally confined to the orientation at which the object is experienced. These results suggest that the ability to skillfully manipulate everyday objects is mediated by multiple rapidly adapting representations which capture the local dynamics associated with specific object contexts.

Conclusion

The methods of sensorimotor neuroscience have traditionally involved the use of artificial laboratory-based tasks to examine the mechanisms that underlie voluntary movement. In the case of visual neuroscience, the adoption of more naturalistic approaches has involved a shift from artificial stimuli created in the laboratory to natural images taken from the real world. Similarly, the adoption of more naturalistic approaches in sensorimotor neuroscience will require a shift from artificial laboratory-based tasks to natural tasks that are representative of the everyday behavior of subjects. Fortunately, continuing advances in motion tracking, virtual reality and even mobile phone technology are making this shift ever more tractable. In the case of visual neuroscience, naturalistic approaches have required new analytical methods from information theory, statistics, and engineering and have led to new theories of sensory processing. Similarly, naturalistic approaches to human sensorimotor control will almost certainly require new analytical techniques, especially with regard to large datasets of natural behavior and movement kinematics. However, we expect that these efforts will be productive.

Acknowledgments

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