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The role of temporal context in perception and action

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Abstract

(English)

Visual information is fundamental to interact with objects. For instance, information is coded by the visual system to create internal representations used to guide actions such as grasping, an action we perform efficiently daily many times. However, how the motor system codes object features for grasping remains poorly understood. In particular, a long-standing debate in the cognitive neurosciences concerns the nature of internal representations of object size during motor preparation, a key aspect of grasping. According to the most influential functional interpretation of the primate visual system, size representations are coded in critically different ways in the dorsal and ventral streams. These key differences in turn have several behavioural consequences, including a relative immunity of the dorsal representations of size from stimulus-contextual effects such as those observed for consciously perceived size. Accordingly, the goal of this thesis is to contribute to the understanding of representations for visually-guided actions by collecting data from psychophysical, kinematics, and EEG paradigms.

I conducted four experiments assessing motor and perceptual responses to the Uznadze illusion. In this illusion, the same ‘test’ object appears larger (or smaller) after having seen a smaller (or larger) ‘inducing’ object. Studies 1 and 2 investigated whether size representations in action and perception are affected by this form of size contrast. In Study 1, participants either grasped a test or provided a perceptual judgment of its size (by performing a cross-modal match called a “manual estimation”) after the presentation of an inducer that could be identical, smaller, or larger. Results revealed that finger apertures in both motor and perceptual responses showed a size contrast effect, that is, were affected by the inducer size. In Study 2, two further manipulations of the Uznadze illusion were investigated. Inducers were presented either haptically or visually, and either in the same or in a different

position relative to the test. Surprisingly, results revealed that motor responses show size contrast (the Uznadze illusion), or size assimilation (the inverse Uznadze illusion), or even no illusion, depending on factors that seem related to multisensory integration and the body schema rather than a perception-action distinction. Overall, Studies 1 and 2 provide evidence that size representations for action are affected by contextual information.

Studies 3 and 4 investigated the time course of motor representations in the dorsal stream. We focussed on the time needed to prepare a grasp, testing whether motor preparation is affected by viewing a previous distractor object equal or different in size. Study 3 showed that participants were slower in preparing the grasp when distractors were larger than the test, but not when they were smaller. Study 4 extended this finding to event-related potentials (ERPs) recordings. Here, cortical indices of motor preparation to grasp the test were investigated after presenting distractors equal or different in size. Results revealed that components of lateralized readiness potentials (LRPs) were displaced in time consistent with the pattern of preparation times observed in Study 3 and 4. Taken together, Studies 3 and 4 show that grasping is not programmed solely from online information, but can be affected by information experienced recently.

I conclude that the Uznadze temporal size contrast reveals that visuomotor preparation relies on relative spatiotemporal information comparable to that used to produce perceptual judgments. This conclusion challenges current theoretical models of the functional properties of the dorsal stream, suggesting a more nuanced view of factors affecting grasping and seeming behavioural perception-action dissociations.

Abstract

(Italian)

La visione è fondamentale per interagire con gli oggetti. Il sistema visivo codifica le informazioni visive per creare rappresentazioni interne che sono usate per guidare azioni come l'afferramento, un'azione che eseguiamo con efficienza molte volte ogni giorno. Tuttavia è poco chiaro come il sistema motorio codifichi le caratteristiche degli oggetti per afferrarli. Nello specifico, un vecchio dibattito nelle neuroscienze cognitive riguarda la natura della rappresentazione della grandezza per afferrare oggetti. Secondo la più influente interpretazione funzionale del sistema visivo dei primati, i flussi dorsale e ventrale codificano la grandezza in modi diversi. Queste differenze hanno diverse conseguenze comportamentali, inclusa una certa immunità delle rappresentazioni dorsali a effetti stimolo-contestuali come quelli osservati nella percezione consci. Lo scopo di questa tesi è di contribuire alla comprensione delle rappresentazioni per l'azione raccogliendo dati in paradigmi di psicofisica, cinematica, ed elettroencefalografia.

Ho condotto quattro esperimenti misurando risposte motorie e percettive all'illusione di Uznadze. In questa illusione, lo stesso oggetto 'test' appare più grande (o più piccolo) dopo aver visto un oggetto 'inducente' più piccolo (o più grande). Gli Studi 1 e 2 hanno indagato se le rappresentazioni della grandezza in azione e percezione sono influenzate da questa illusione. Nello Studio 1 i partecipanti afferravano il test o ne giudicavano la grandezza (eseguendo un confronto cross-modale chiamato 'stima manuale') dopo aver visto un inducente che poteva essere identico, più piccolo, o più grande. I risultati hanno rivelato che in entrambe le risposte motorie e percettive le aperture delle dita mostravano il contrasto di grandezza, cioè erano influenzate dalla grandezza dell'inducente. Lo Studio 2 ha esaminato due ulteriori manipolazioni dell'illusione di Uznadze. Gli inducenti erano presentati apticamente o visivamente, nella stessa posizione del test o in una diversa. I

risultati hanno rivelato che le riposte motorie mostrano contrasto di grandezza (l'illusione di Uznadze), assimilazione di grandezza (l'illusione di Uznadze inversa), o nessuna illusione. Questo sembra dipendere da fattori legati all'integrazione multisensoriale e allo schema corporeo, piuttosto che a una distinzione fra azione e percezione. Complessivamente, gli Studi 1 e 2 provano che la codifica della grandezza per l'azione è influenzata da informazioni contestuali.

Gli Studi 3 e 4 indagavano il decorso temporale delle rappresentazioni motorie nel flusso dorsale. Abbiamo valutato se il tempo necessario per preparare una presa fosse influenzato dalla vista di un precedente oggetto distrattore di uguale o diversa grandezza. Lo Studio 3 ha mostrato che i partecipanti erano più lenti nel preparare la presa quando i distrattori erano più grandi del test, ma non quando erano più piccoli. Lo Studio 4 estende questo risultato a registrazioni di potenziali evento-reati (ERPs). Abbiamo esaminato indici corticali della preparazione motoria per afferrare il test dopo la presentazione di distrattori di uguale o diversa grandezza. I risultati hanno rivelato che componenti dei potenziali di preparazione lateralizzati (LRPs) erano spostati nel tempo in linea con i tempi di preparazione. Questi studi assieme mostrano che l'afferramento non è programmato solo online ma può essere influenzato da informazioni precedenti.

Concludo che il contrasto di grandezza temporale di Uznadze rivela che la preparazione visuomotoria si basa su informazioni spazio-temporali contestuali confrontabili a quelle usate per i giudizi percettivi. Questa conclusione contraddice i modelli attuali sulle proprietà funzionali del flusso dorsale, suggerendo una visione più sfumata dei fattori che influenzano l'afferramento e delle apparenti dissociazioni fra percezione-azione.

Preface

The research reported in this thesis has been conducted at the Department of Medicine and Surgery - Unit of Neuroscience of the University of Parma (IT). The only exception is the study presented in Chapter 5 that was conducted at the Department of Psychology of the Liverpool Hope University (UK).

Most of the work presented in this thesis was written to be published as independent articles. To date (December 2020), three of these articles have been published, the other one is in preparation. Each chapter from 2 to 5 consists of one of those articles. The advantage is that each chapter stands by its own and it can be read alone. The disadvantage is that some overlaps or repetitions in theoretical background may occur. I think, however, that this does not make tough the readability of the thesis but it rather helps to hold the thread along the chapters.

Chapter 2 has been published as

Uccelli, S., Pisu, V., Riggio, L., & Bruno, N. (2019). The Uznadze illusion reveals similar effects of relative size on perception and action. *Experimental Brain Research*, 237(4), 953-965.

Chapter 3 is in preparation

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Parts of this thesis were presented at symposia and conferences as talks or posters

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Uccelli, S., Pisu, V., Palumbo, L., Harrison, N., & Bruno, N. Asymmetric effect of distractor graspable objects on lateralized readiness potentials of successive actual grasps. The 42st European Conference on Visual Perception, Leuven, 2019. *Perception*. 2019;48(2_suppl), 1-236.

Uccelli, S., Pisu, V., Garofalo, G., Riggio, L., & Bruno, N. "Grasping the Uznadze illusion: hand shaping is driven by relative size as well as stimulus similarity". The 41st European Conference on Visual Perception, Trieste, 2019. *Perception*, 48(1_suppl), 117.

Pisu., V., Uccelli, S., Riggio, L., & Bruno, N. Asymmetric effect of distractor graspable objects on successive actual grasps. The 41st European Conference on Visual Perception, Trieste, 2018. *Perception*, 48(1_suppl), 117.

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Chapter 1

General introduction

We interact with our world predominantly using visual information. Vision is indeed essential to recognize the features of objects and use them for different aims. For instance, we may recall how an object looks to verbally describe its features to someone, or to distinguish an object from another. But we use visual information about objects also for guiding actions such as grasping, which represents a distinctive skill in humans. We grasp objects countless times for many daily purposes as, for instance, picking up a coin, holding a pen for writing, or drinking from a cup. Firstly, the interaction starts from how we grasp the object with the hand. A fast glance at the object is usually enough to have an idea of how to grasp it, then we rapidly shape the hand in a such way as to achieve an effective and effortless grip most of the time. Described in this way, grasping seems easy to perform, but actually it requires coding object features in advance and solving several non-trivial issues of motor control. In particular, it is unclear how visual information of objects, such as size, is coded in the motor system for guiding grasps.

Studying how the motor system codes visual information is important because the goal of vision is to code such information in such a way as to build internal representations of the world (Bruce, Green, & Georgeson, 2003). Under particular circumstances, however, such representations may not correspond to the real world, resulting in inaccurate and unreliable percepts (Gregory, 1997; Coren & Girgus, 2020). This may happen because perception generates context-based representations by comparing objects in the visual scene to each other. Thus, features such as size, color, length, and others are perceived relative to surrounding elements. Research in psychology is rich in examples of such relational determination. Famously, the human eye is fooled by illusions that make objects appear different from how they actually are (Shapiro & Todorovic, 2016; Robinson, 2013; Gilliam, 1998). For instance, we judge an object as larger than its actual size when it is surrounded by smaller objects. Although visual illusions are typically studied in visual perception, their effect can be investigated also in the motor system. Suppose to grasp an

object that appears larger than its real size. Will the fingers open accordingly with the perceived or the physical size of the object? It has been claimed that actions are relatively unaffected by visual illusions compared to conscious perception. In cognitive neuroscience, this claim represents has represented a landmark on visuomotor transformations supporting, the general idea that size representations in action rely on mechanisms different from those implied in perception.

In this thesis, I carried out four experiments collecting data from psychophysical, kinematics, and EEG paradigms. The aim was to investigate how the size representation for actions is coded starting from visual information. For this purpose, I assessed motor and perceptual responses to the Uznadze illusion. In this introductory chapter, I will summarize theories on the processing of visual information for perception and action. Next, I briefly report both supportive and contrastive evidence gathered in the last years. Finally, I outline an overview introducing the reader to the issues tackled in the next chapters.

The two visual systems

That the visual system of many animals can be subdivided in two modular subparts is not a new claim. However, the functional interpretation of these two subparts was the subject of debate. The first interpretation dates back to the end of the sixties from studies on animal models. Schneider (1969) removed visual cortical structures in hamsters (areas 17 and 18) making them unable to orient in space but sparing their ability to discriminate visual patterns. Disconnecting tectal regions from the superior colliculus, instead, caused hamsters to show the opposite pattern. This finding suggested the presence of two visual structures characterized by different processing: A cortical system coding object recognition and one other, subcortical system coding spatial coordinates. Similar conclusions were drawn also from studies on monkeys (Trevarthen, 1968) and frogs (Ingle, 1973).

In the eighties, Ungerleider and Mishkin (1982) proposed a functional interpretation of the two separate streams both originating from the primary visual cortex (V1). One is called ‘ventral stream’ and projects toward inferotemporal areas (IT); the other one is called ‘dorsal stream’ and projects toward posterior parietal areas (PPC). Lesions to IT areas made the monkey unable to discriminate objects having different shapes, whereas lesions to PPC areas made the monkey unable to discriminate the position of an object in space. The authors concluded that the ventral stream codes the visual recognition of an object while the dorsal stream codes the spatial collocation of that object. Through the years, the ventral and dorsal streams were interpreted as the ‘what’ and ‘where’ systems, respectively.

In the nineties, Milner and Goodale (1992) proposed a new interpretation that had a great impact on cognitive neuroscience. In their view, the ventral stream remains responsible for recognition and identification; It codes object properties such as size, orientation, shape, and color, which are essential features for representing the three-dimensional structure of an object. Thus, their proposal does not differ too much from that delineated by Mishkin, Ungerleider, & Macko (1983). However, Milner and Goodale put more emphasis on how the two streams transform visual information for different purposes. In their theory, the dorsal stream is responsible for the visual control of object-directed actions, rather than coding only spatial coordinates. In other terms, the ventral stream codes visual information for recognizing objects (“what” system) while the dorsal stream codes visual information for control actions directed to those objects (“how” system). For this reason, the former is often called “vision-for-perception” and the latter “vision-for-action” (Figure 1.1), and Milner and Goodale’s proposal is called the ‘two-visual-system-hypothesis’, or TVSH for short.

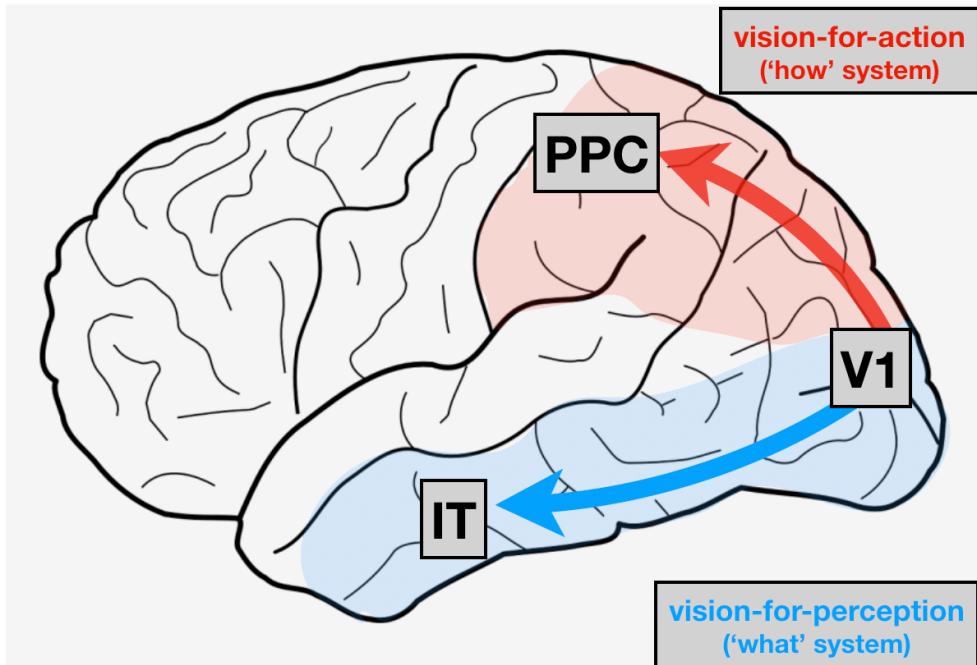


Figure 1.1. A schematized representation of the two-visual-systems hypothesis (TVSH). Arrows represent the dorsal and ventral cortical visual streams (or pathways) both originating from the primary visual cortex (V1): The red one represents the vision-for-action system directed toward the posterior-parietal cortex (PPC); The blue one represents the vision-for-perception system directed toward the inferotemporal cortex (IT).

According to the TVSH, vision-for-perception operates with allocentric frames of reference. Objects are coded relative to other objects in the visual scene, independently from where our body is or changes in viewing conditions. Such a mode of operation allows to recognize objects, to verbally describe them, and to keep their representations in mind for recall them later if necessary. Accordingly, vision-for-perception possesses long-term memory. In contrast, vision-for-action operates with egocentric frames of reference that code the relationship between the object and the action's effector. In grasping, for instance, we need to know in advance the position in the space of both the object and our hand. However, we can rapidly move our hand such that vision-for-action needs to continuously compute the coordinates of both the object and hand over time supplying online information for the ongoing action.

Accordingly, vision-for-action possesses a much more immediate, short-lived memory.

The aforementioned concepts will appear again in the next chapters, as they represent part of the theoretical framework for the experiments of this thesis. In the following two paragraphs, I summarize evidence and controversy of the TVSH from two kinds of literature: The first on neuropsychological patients, and the second on behavioural dissociations in healthy people.

Evidence from patient studies

Evidence for the TVSH has come firstly from studies on patients having brain lesions. In neuropsychology research, if a lesion in a specific brain area interferes with a specific behaviour, that area is assumed to be responsible for that behavior. Milner and Goodale reported extensive studies on the famous patient D.F., who suffered damage to occipito-parietal areas after carbon monoxide poisoning (Goodale et al., 1991; Goodale et al., 1994). When asked to verbally describe a target object, D.F was not able to report object features such as its size, color, shape, or orientation (Humphrey et al., 1994; 1995; Carey, Harvey, & Milner, 1996). Such neuropsychological disorder is referred to as ‘apperceptive’ or *visual form agnosia* (Milner et al., 1991). Surprisingly, when D.F was asked to grasping the same object her performance was substantially intact and similar to that of people without brain lesions; Her finger aperture was indeed correctly scaled on the object size. In short, a patient with ventral damage is unable to perceive and therefore recognize the properties of an object, but may be capable of visuomotor processes for object-directed actions.

Visual form agnosia was interpreted as evidence of separate codings in the two visual streams. However, the hypothesis of separate codings would be strengthened by observing a behaviour opposite to that of D.F. in the

presence of dorsal damage. Indeed, patients having lesions in parietal areas show a neuropsychological disorder known as *optic ataxia* (or Balint's syndrome; Balint, 1909). In contrast to D.F., these patients failed when asked to pick-up objects, showing that fingers were not correctly adjusted to the shape and size of the target object. But when asked to verbally describe the same object (such as, for instance, report the size or the orientation), their performance was quite accurate. In short, patients with optic ataxia fail in performing actions due to dorsal damage, but still maintain access to perceptual knowledge of the object (Perenin & Vighetto, 1983; 1988; Jakobson et al., 1991; Milner et al., 1999). Taken together, visual agnosia and optic ataxia constitute a 'double dissociation' between ventral and dorsal systems representing key evidence for the TVSH.

Despite anatomical and neuropsychological arguments in favor of a double dissociation, several criticisms have been raised successively. For instance, Rizzolatti and Matelli (2003) proposed a model involving three main pathways: the ventral stream (v), the ventro-dorsal stream (v-d, formed by MT area and the inferior parietal lobule, IPL), and the dorso-dorsal stream (d-d, formed by V6 area and the superior parietal lobule, SPL). According to these authors, the ventral stream is responsible for perceptual awareness as proposed in previous theories. The v-d stream, instead, is responsible for integrating information from different sensory areas to organize actions, whereas the d-d stream mainly controls 'online' processing while actions unfold. In short, these authors claimed a partial communication between ventral and dorsal processing in the v-d stream. Rossetti, Pisella, & Vighetto (2003) revised the results on patients claiming that the collected data was insufficient in support of a double dissociation. The authors argued that a rigid dichotomy is unlikely to explain such complex disorders, suggesting instead an organization with multiple parallel sub-streams for multiple visuomotor integrations (Rossetti & Pisella, 2002; Pisella et al., 2006).

Last, a more complex picture resulted from successive tests on the patient DF. For instance, DF's grasping was accurate only when she received haptic feedback (Schenk, 2012) or when the target was presented in central vision (Hesse, Ball, & Schenk, 2011); thus, without haptic information, or with targets presented in peripheral vision, her performance was similar to that of patients having optic ataxia. These findings suggest that a single patient can no longer be considered as a model for testing the neural basis of action-perception dissociations (but see Ganel & Goodale (2019), in which they reported that DF's performance was overall in accord with a double dissociation).

Action-perception dissociations in neurotypical individuals

We have seen that double dissociations in patients represents key evidence for the TVSH. However, cortical lesions rarely interest one restricted region but rather involve more extended structures. Thus, behavioral findings on patients might result from a complex mixture of several deficits. For this reason, much research on the action-perception dissociation has moved to investigating healthy individuals.

A branch of this research has focussed on the effect of visual illusions in perception and action. The first study was authored by Aglioti, DeSouza, and Goodale (1995). They presented to participants a double-display version of the well known Ebbinghaus-Titchener illusion. This consists of two central disks having the same diameter, one surrounded by an array of larger disks and the other one by an array of smaller disks. This creates a size-contrast illusion in which the first disk is perceived as smaller and the second disk as larger (Figure 1.2a). Participants performed perceptual and motor tasks. In the former, they verbally reported which disk appeared larger. In the latter, they grasped that disk with their right hand. Results revealed that perceptual judgments were deceived by the illusion (i.e., they chosen the 'enlarged'

central disk). However, the maximum grip aperture (MGA) when grasping the disk was scaled on its actual size. Consistent results were found when participants provided a manual estimate (ME) of the perceived disk size; MEs were smaller (or larger) for the central disk surrounded by an array of larger (or smaller) disks, whereas MGAs did not vary across arrays (Haffenden & Goodale, 1998; 2000; Haffenden, Schiff, & Goodale, 2001). In short, perceptual judgements appeared to be affected by the Ebbinghaus illusion whereas grasping did not. The authors claimed that vision-for-action is immune to illusions, in contrast to vision-for-perception. Thus, this finding represented a key evidence of distinct codings between the two streams as claimed by the TVSH.

However, later works reported results that can not be easily explained by the TVSH. For instance, Franz et al. (2000) claimed that the dissociation observed by Aglioti and colleagues resulted from methodological confounds between perceptual and motor tasks. In the experiment of Aglioti et al., participants had available both the two Ebbinghaus arrays during the judgement of the size, en chaining the illusion effect between the two central disks. In other words, the judgement involved a comparison (relative sizes), whereas the grasping was focused only one source of information (that might be thought of as an absolute size) neutralizing the illusory effect. When tasks were performed using only on one configuration of the Ebbinghaus illusion, perceptual and motor responses revealed similar illusory effects (Franz et al., 2000; Pavani et al., 1999; see also Plodowski & Jackson, 2001). More recently, a multi-lab study (Kopiske et al., 2016) collected data from a large sample of participants presenting them with a single display of the Ebbinghaus illusion. Results showed that MEs and MGAs were affected by the illusion in a comparable way. In addition, Kopiske at al (2016) demonstrated that MGAs were not affected by the distance of the surrounding circles (i.e., the obstacle avoidance hypothesis, see Haffenden, Schiff & Goodale, 2001). Although this study represents strong evidence against

action-perception dissociation in grasping, proponents of the TVSH criticized the work of Kopiske and colleagues on several points (for details, see Whitwell & Goodale, 2016, & Kopiske et al., 2017).

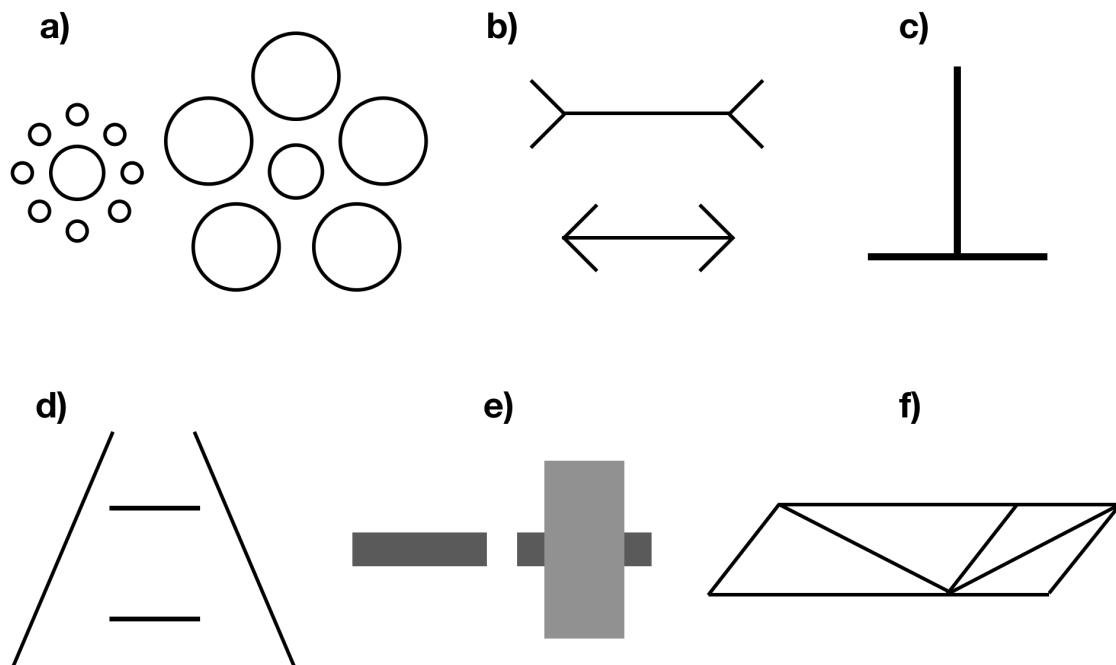


Figure 1.2. Examples of visual illusions used to test action-perception dissociations. a) Ebbinghaus-Titchener illusion (both central disks have the same diameter, but the one surrounded by small circles is perceived as larger); b) Müller-Lyer illusion (the two horizontal lines have the same length, but the one with arrows pointing outside is perceived longer); c) horizontal-vertical illusion (both lines have the same length, but the vertical one appears longer); d) Ponzo illusion (the upper horizontal segment appears longer than that below although they are identical); e) Kanizsa's compression illusion (both black rectangles have the same length, but the one covered by the grey shape appears shorter); f) Sander's parallelogram illusion (both diagonals have the same length, but the left one appears longer).

The effect of the Ebbinghaus illusion on grasping inspired researchers to further investigate action-perception dissociations in healthy people. Thus, many other visual illusions have been employed in paradigms involving perceptual and motor tasks as, for instance, the Müller-Lyer illusion (Figure 1.2b) (Bruno, Knox, de Grave, 2010; Bruno & Franz, 2009; Bruno, Bernardis,

& Gentilucci, 2008; Bernardis, Knox, & Bruno, 2005), the horizontal-vertical illusion (Figure 1.2c) (Vishton et al., 1999), the Ponzo illusion (Figure 1.2d) (Brenner & Smeets, 1996; Jackson & Shaw, 2000; Whitwell et al., 2016), the Kanizsa's compression illusion (Figure 1.2e) (Bruno & Bernardis, 2002), and Sander's parallelogram illusion (Figure 1.2f) (Whitwell et al., 2018; Smeets et al., 2020; Carter-Krone, Senanayake, & Marotta, 2020). Some of these studies have confirmed the absence of illusory effects on grasping; other studies, instead, found reliable illusory effects on grasping which were comparable to perceptual responses. Thus, a controversial literature has been collected (for reviews, see Gorea & Cardoso-Leite, 2010; Franz & Gegenfurtner, 2008; Smeets & Brenner, 2006).

Alternative theories

We have seen that the literature on patients and neurotypical individuals does not converge into a clear picture, leaving open many questions. In this paragraph, I briefly report alternatives to the TVSH which are useful to understanding the methodological approach used in the next chapters.

Bruno (2001) proposed that the critical distinction is not between which type of response is used (perception vs. motor) but between which frame of reference that response demands. A perceptual report as the manual matching emphasizes the object size relationships with the surrounding visual scene, whereas a motor response such as grasping emphasizes the relationship between the object and the viewer's hand. Accordingly, it would be possible to obtain both illusory and veridical responses from the same perceptual or motor response depending on which frame of reference (object-centered vs. effector-centered) is emphasized in the task. According to Bruno, therefore, the selection of a specific frame of reference might explain visuomotor dissociations, suggesting that the functional properties of vision-for-perception and vision-for-action are less different than proposed by the TVSH.

Franz (2001) suggested a common source of information that generates an internal representation that feeds actions as well as perception. Accordingly, visuomotor dissociations in healthy participants would result from methodological artifacts and confounds. When tasks are designed to avoid such issues, perceptual and motor responses are similarly affected by illusions. For instance, Franz highlighted the issue of how to compare perceptual and motor responses. ME and MGA indeed show different responsiveness to a physical variation of object size. MEs have a slope of 1 or even greater (1.57 according to Franz, 2003). Instead, MGAs have a slope of 0.82, as determined by Smeets and Brenner (1999). For this reason, given an illusion that produces an illusory effect of 1 mm, for MEs this would correspond to a $1 / 1.57$ mm change in the physical size, whereas for MGAs would correspond to $1 / 0.82$. Franz and colleagues claimed that is erroneous to compare illusory effects between measures having different scaling, suggesting that corrections must be applied before comparing (i.e., the ‘corrected’ illusion effect, Franz, 2003; Franz et al., 2001; see also Bruno & Franz, 2009).

The idea of a common source of information would be strengthened if the V1 surface correlates with the magnitude of visual illusions. If size-contrast effects were already coded in V1 (i.e., in a very early stage of the visual processing) would weaken the assumption that vision-for-perception and vision-for-action process the same information in different manners. To date, two fMRI studies support this idea. Schwarzkopf, Song, & Rees (2010) found that the magnitude of the Ebbinghaus and Ponzo illusions was indeed correlated with V1 surface. Murray, Boyaci, & Kersten (2006) found that an object that appears to occupy a larger portion of the visual field activates a larger area in V1 than an object with the same angular size that is perceived to be closer and smaller. Although based only on two studies, these results

suggest that basic aspects of our consciousness such as the perceived size are directly reflected in V1.

Last, Glover (Glover, 2004, 2002; Glover & Dixon, 2001a) proposed the intervention of two different visual representations between the planning and control phases of a movement (i.e., the planning-control model). The distinction between planning and control is not new and represents an important aspect of motor control (Woodworth, 1899; Jeannerod, 1988). According to this model, the planning module codes kinematics parameters of grasping based on a context-dependent representation before movement initiation; then, once the movement is initiated, the control module enters in play correcting grasp kinematics online based on a context-independent representation. Thus, actions show illusory effects in the early preparation stage, but such effects are nullified by online corrections during the ongoing movement. Studies in support of the planning-control model have shown that the inferior-parietal lobule (IPL) is more active during planning, whereas the superior-parietal lobule (SPL) is more active during action execution (Deiber et al., 1996; Desmurget et al., 1997, 1999).

At this point, the reader may draw the conclusion that the TVSH as it is currently stated should be reformulated. Milner and Goodale, indeed, acknowledged that vision-for-perception and vision-for-action can interact with each other, and that grasping can show illusory effects on some occasions (Milner & Goodale, 2008; Milner, 2017). Notwithstanding, nowadays the TVSH still represents a landmark in research on visuomotor transformations and several criticisms remained unexplained (for instance, see Grünbaum, 2018; Rossetti, Pisella, & McIntosh, 2017; Schenk & McIntosh, 2010).

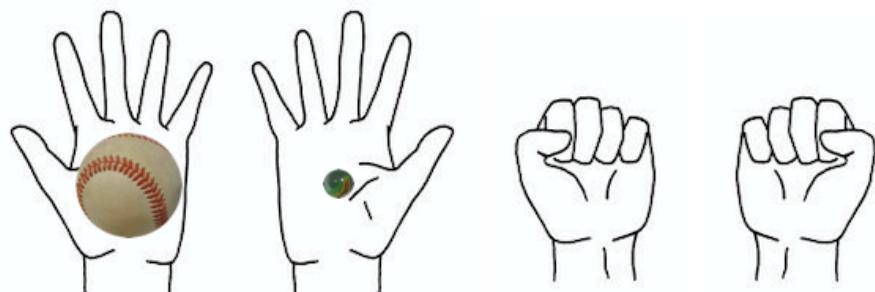
The Uznadze illusion

The research reported in the next chapters has been carried out using the (partially) unexplored Uznadze illusion. Originally described in haptics by Uznadze (1966), this illusion consists of a powerful sequential contrast easily detectable by anyone. Imagine to hold a large ball in one hand and a small ball in the other hand, and to squeeze them a few times ('adapting' or 'inducing' stimuli); then, the two balls are replaced with two, medium identical balls ('induced' or 'tests' stimuli) (Figure 1.3). Although they have the same size, the test ball preceded by the small inducer is perceived as larger, while the test ball preceded by the large inducer is perceived as smaller. The effect is obvious and easy to replicate across and within individuals.

The 'Uznadze effect' manifests in several sensory modalities, and many scientists attempted to explore its mechanisms further (Maravita, 1997; Kappers & Bergmann-Tiest, 2014; Calzolari et al., 2017; Bruno et al., 2018; Daneyko, Maravita, & Zavagno, 2020). Although these studies documented the robustness and reliability of the illusion, it has not been studied in motor tasks. The Uznadze illusion represents a promising candidate to test action-perception dissociations at least for three, encouraging reasons. First, the magnitude of the illusion in vision is quite strong (~ 5-10% in perceived size relative to actual size); Thus, it is easier to detect illusory effects in grasping. Second, it involves a temporal context between two stimuli rather than a static array as most of the illusions previously tested. Given this, therefore, this illusion challenges also models that attribute to vision-for-action a short-term memory for supplying online processing of information (Westwood & Goodale, 2003). Third, the temporal display lends itself to further interesting manipulations. For instance, the inducing stimulus could be presented in a different sensory channel than that of the induced stimulus, or the two stimuli could be presented in two different spatial positions. In brief, this illusion offers

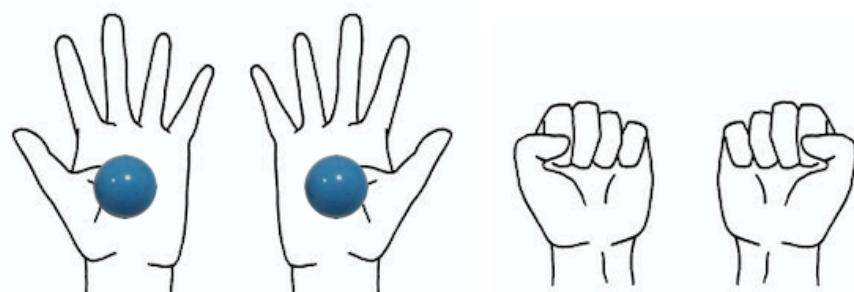
many options for investigating spatiotemporal aspects of visuomotor processes for actions.

adapting / inducing balls



hands opening and
closing a few times

induced / tests balls



which ball is larger?

Figure 1.3. A graphical representation of the Uznadze illusion in haptics. Upper panel: two ‘adapting’ or ‘inducing’ balls of different sizes are put in participant’s hands while he or she keeps the eyes closed. Then, he or she squeezes the balls a few times by closing and opening the hands around the balls’ surface. Lower panel: The experimenter replaces quickly the two inducing balls with the two ‘induced’ or ‘test’ balls identical in size. With eyes still closed, the participant tightens the balls the last time and verbally reports which ball he or she feels as larger.

Summary and research questions

In this paragraph, I outline the major questions which I have tried to answer with the studies reported in the next chapters. All of them have been conducted by using slightly different versions of the Uznadze illusion. The first two (chapters 2 and 3) focus on the size representation in grasping computed from visual information. The last two (chapters 4 and 5) focus on motor preparation and memory-related issues in grasping.

Chapter 2. This is the first work in which the Uznadze illusion was used in a motor task. The main goals were to test whether the size representation in grasping is affected by this illusion and to compare this to perceptual responses. Besides, this work explores whether size representation in grasping is sensitive to the visual similarity between two objects related in time. This work tries to answer the following question: do vision-for-perception and vision-for-action “read-out” the size of an object in a similar fashion?

Chapter 3. This work also regards size representation in grasping but presenting the Uznadze illusion in two further manipulations. Specifically, I investigated whether the haptic exploration of the inducing stimulus produced the same Uznadze effect on both perceptual and motor responses as in the vision system. Besides, I also investigated whether the illusory effect manifests when the inducing stimulus is presented either in the same position of the induced stimulus or in a different position. This study reveals that both perceptual and motor responses can show the Uznadze effect, a reverse Uznadze effect, or no illusion at all depending on whether the inducing stimulus was presented haptically or visually and in the same spatial position or not.

Chapter 4. This work focuses on the temporal aspects of grasping. Here, the Uznadze illusion was used to investigate a different issue: is the motor

preparation for grasping a target object affected by the sight of a previously presented object having a different size? The core idea is that the mere observation of a graspable object elicits an internal representation of the appropriate grip. Thus, this could have an effect on motor preparation for grasping a successive different object. The novel results of this study challenge the current view on motor control stating that actions rely only on online information disregarding the context experienced in the recent past.

Chapter 5. Last, this work aims to corroborate the behavioural findings of Chapter 3. Involving the same paradigm, I investigated event-related potentials (ERPs) during a pantomimed grasping task. Specifically, I found that the time course of the lateralized readiness potential (LRP, i.e. an online cortical signature of motor preparation) was displaced in time depending on the size of the previous distractor object. This finding confirms that actual motor representations do not decay immediately but are rather affected by the previously presented context.

Chapter 2

The Uznadze illusion reveals similar effects of relative size on perception and action

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Abstract

Milner and Goodale (the visual brain in action, Oxford University Press Inc., Oxford, 1995) proposed a functional dissociation between vision-for-action and vision-for-perception (i.e., the “two-visual system hypothesis”, TVSH). Supporting the TVSH, it has been claimed that visual illusions affect perception but not actions. However, at least for the Ebbinghaus illusion, numerous studies have revealed consistent illusion effects on grasping. Thus, whether illusions affect actions remains controversial. To further investigate the dissociation predicted by the TVSH, we used a visual version of the Uznadze illusion (the same stimulus will feel smaller after feeling a larger stimulus and larger after feeling a smaller stimulus). Based on kinematic recordings of finger aperture in a motor (precision grip) and a perceptual task (manual estimation), we report two main findings. First, both action and perception are strongly affected by the Uznadze illusion. Second, the illusion decreases similarly in both tasks when inducing-induced pairs had different shape and color, in comparison to the equivalent condition where these features are the same. These results are inconsistent with a perception–action dissociation as predicted by the TVSH and suggest that, at least in the present conditions, vision-for-perception and vision-for-action are similarly affected by contextual cues.

Introduction

The primate visual system shows two streams of projections from the primary visual area: A ventral projection to the inferotemporal cortex and a dorsal projection to the posterior parietal cortex. Is this dorsal-ventral split a mere anatomical distinction, or does it reflect a functional specialization of visual processing? Ungerleider and Mishkin (1982), famously proposed that the ventral stream specializes in processing object identity, whereas the dorsal stream codes space (“what” vs. “where”). Milner and Goodale (1995, 2006, 2008), Goodale and Milner (1992) updated this early suggestion, proposing that the ventral stream codes spatial and object features that are useful for recognition, whereas the dorsal stream codes spatial and object features aimed at guiding movements (“vision-for-recognition” vs. “vision- for-action”). In Milner and Goodale’s view, the dorsal and the ventral streams are not merely a manifestation of how the visual system codes different kinds of stimulus features (object- vs. space-related). The two streams are instead assumed to reflect separate modules that use the available visual information for different purposes. For instance, object properties such as orientation, size, and shape can be used, within appropriate spatial frameworks, to represent the three-dimensional structure of an object for the purpose of matching it to a structural representation in memory and attain recognition (Biederman 1987). Alternatively, orientation, size, and shape can be used, within different spatial frameworks (Bruno 2001), to feed the motor system parameters that can be used online to code the trajectory and the pre-shaping of the hand while approaching the object with the ultimate goal of grasping it.

The proposal of Milner and Goodale is often referred to as the “two visual system hypothesis” (TVSH). According to the TVSH, vision-for-recognition provides a conscious and detailed representation of the world that we can describe with words. This process is relatively slow and privileges object-relative frames of reference that are used to compute constant object descriptions under variations of stimulus conditions. In contrast, vision-for-

action implements sensorimotor mechanisms for planning and executing object-directed actions. Vision-for-action is faster, can be unconscious, and uses effector-relative frames of reference as appropriate for controlling movements. According to the TVSH, therefore, the two streams possess different coding mechanisms that lead to a functional dissociation between perception and action. Vision-for-perception emphasizes relational information that mediate object constancy. Relevant relations involve elements that are simultaneously present across space within the visual field (e.g., an object surrounded by other objects), but also, crucially, elements that are presented over time (e.g., an object preceded by another object in the same location) as the spatial representations in this subsystem are held in memory for a relatively long time. Conversely, spatial codes for actions emphasize the current relationship between a target object and the observer's effector, but this representation is relatively short-lived as it needs to be continuously updated as the action proceeds. Given these functional differences, one would expect that different tasks requiring spatial or temporal frames of reference for perception and action should result in different measurable outputs from the same visual information. Said otherwise, it would be expected that perception-action dissociation will be observed between tasks that are based on the same visual information, but require motor vs. perceptual responses.

Support for the dissociation between vision-for-action and vision-for-perception has come from monkey and human studies employing several different techniques (for reviews, see Goodale 2011; Carey 2001; McIntosh & Schenk 2009; Whitwell et al. 2014). In particular, a double dissociation between object recognition and object manipulation has been reported in patients with visual form agnosia and optic ataxia (Milner et al. 2001; Goodale & Milner 1992), suggesting that ventral lesions can affect conscious perception but not object-directed actions, whereas dorsal lesions can preserve object recognition while interfering with actions programming. However, to what extent neuropsychological data supports the TVSH is still controversial (for differing opinions, see Rossetti & Pisella 2002; Pisella et al.

2006; Milner et al. 2012; Goodale 2008; Milner & Goodale 2008; Schenk 2006, 2010, 2012; Bruno et al. 2008, 2010; Bruno & Franz 2009; Cardoso-Leite & Gorea 2010). In behavioral studies with healthy participants, it has been reported that perception is affected by the Ebbinghaus size-contrast illusion, whereas grasping is not (Aglioti et al. 1995; Haffenden and Goodale 1998; Haffenden et al. 2001). However, this specific finding also remains highly controversial (Bruno 2001; Franz 2001, 2003; Smeets and Brenner 2006; Schenk et al. 2011; Kopiske et al. 2016; but see, Whitwell & Goodale 2016). In this paper, we provide a novel test for the action-perception dissociation predicted by the TVSH. To this aim, we begin by reviewing studies that used a grasping task in the context of an illusion display.

Testing the TVSH: grasping visual illusions

The seminal study on perception-action dissociations in behavioral tasks by healthy participants was conducted by Aglioti, DeSouza, and Goodale (1995). In the Ebbinghaus size contrast illusion, a central disk surrounded by larger (or smaller) context disks is perceived as being smaller (or larger) than a comparison disk without a context. Aglioti and collaborators asked if the representation of size used to guide a grasping movement would be similarly affected by the context. Based on the TVSH, one might predict that it would not, as the spatial frame of reference for guiding the action is assumed to be centered on the effector and disregard the scene context. In their experiment, Aglioti et al. presented two target disks in two different versions of the Ebbinghaus display. In one version, targets were physically identical but perceived as different, whereas in the other they were physically different but perceived as identical (this second version was made possible using a slightly larger target in the context of the large disks, and a slightly smaller one in the context of the small disks). They requested participants to pick up the disk on one side if they thought the disks were different or to pick up the disk on the other side if they thought they were the same (the two versions were

presented randomly, and sides were also counterbalanced). Results showed that participants generally picked up the disk matching the appropriate versions of the display (for instance, they choose the side signifying “different” in the illusion version), which indicates that their perceptual awareness was affected by the context disks. However, grasping parameters did not reflect these perceived differences. Instead, the maximum in-flight aperture of the fingers before touching the disks were scaled to the actual size: On average, participants opened their fingers about equally when the disks were perceptually different due to small or large contexts, but physically the same; conversely, they opened them more (or less, as was appropriate) when the disks looked the same but were in fact physically different. Thus, Aglioti et al. concluded that the visual representation of size used to drive grasping is different from the representation used for perceptual recognition.

The findings of Aglioti et al. have been criticized on several grounds. A first criticism pertains to the asymmetry between the perceptual and motor tasks in terms of attentional demands (Pavani et al. 1999; Bruno 2016; Franz et al. 2000). When participants evaluated whether the disks were the same or different, they had to move the attentional focus from one disk to the other to perform the comparison. When they then performed the grasp, however, they needed to pay attention only to the disk on the side corresponding to the selected response. Thus, the observed size contrast effect may have been determined by both contexts in the perception phase of the response, but only by one in the action phase. This may have artefactually reduced the size contrast effect in the motor task, making it harder to detect a significant difference. A second critical aspect is the absence of an appropriate perceptual measure to compare to grasping (Franz, 2003). For this reason, several studies (for instance, Daprati & Gentilucci 1997; Haffenden & Goodale 1998) have used a modified perceptual task, whereby participants report perceived size by adjusting the distance between the finger and thumb without moving the hand forward. This “manual estimation” task, essentially a form of cross-modal matching (Stevens, 1957), has the advantage of equating

attentional demands but is not itself free of problems as we will see shortly. Last, but not less important, in their experiment Aglioti et al. asked participants to perform the tasks with full visual feedback during the action (i.e., they used a closed-loop procedure). It is known that relatively simple actions such as grasping can be divided into an initial, ballistic phase, and a slower control phase. The initial phase reflects the initial program, whereas the control phase uses feedback loops to refine and conclude the movement (Woodworth, 1899). In consequence, in the experiment of Aglioti et al., the size-contrast effect on grasping may have decreased due to fine adjustments during this control phase as visual information was continuously available.

However, even after several studies that controlled the above experimental artifacts, there is still no consensus view as to whether perception and action can be dissociated in the context of illusions, under what conditions, and what are the implications for the TVSH (Pavani et al. 1999; Franz et al. 2000; Franz & Gegenfurtner 2008; Schenk & MacIntosh 2010; Kopiske et al. 2016; Rossetti & Pisella 2002; Rossetti et al. 2017; Whitwell et al. 2018). In the present study, we used a previously unexplored illusion, the Uznadze size contrast display, to perform a novel test of the TVSH predictions. We chose to use the Uznadze illusion for two reasons. First, the Uznadze illusion consists of a much stronger perceptual effect than the Ebbinghaus illusion. This means that it should be easier to demonstrate a dissociation between perception and action if one predicts that action should be immune from it. Second, unlike the Ebbinghaus display, the Uznadze illusion involves a sequential contrast. In the next section, we argue that this type of contrast represents a formerly untested aspect of the action–perception dissociation predicted by the TVSH.

The Uznadze illusion

The Uznadze illusion (Uznadze, 1966) is a powerful sequential contrast effect originally described with haptic stimuli. In Uznadze’s original setup, participants grasp two balls, a large ball with one hand and a small one with the other. After exposure to these two (“adapting” or “inducing”) balls, they

receive two identical medium-sized balls. As one would expect, these two target (or “induced”) balls do not feel to have the same size (although they are physically the same): The target preceded by the large ball feels smaller and the target preceded by the small ball feels larger. The difference is quite obvious and is readily reported by anyone who is exposed to the effect. Less obviously, however, the perceived difference does not depend merely on the local contrast signal between the inducing and the induced stimulus sizes but includes subtler contextual effects. In a recent study, for instance, Kappers and Bergmann-Tiest (2014) asked what would happen if the inducing and induced stimuli were not the same 3D shape. Thus, they presented participants with spheres and later tested them again with spheres (i.e., congruent condition) or presented spheres but later tested with tetrahedra (i.e., incongruent condition). They observed that size contrast was stronger with congruent pairs and weaker with incongruent ones. They interpreted this as evidence that perceived size does not depend solely on relative stimulus sizes and that high-level, cognitive factors also come into play.

However, Bruno et al. (2018) recently noted that a simpler explanation for these congruency effects is in terms of mid-level perceptual organization rather than high-level cognition. According to this idea, local relational signals, such as relative sizes, are given stronger or weaker weights based on a rule of perceptual unit formation, such as the Gestalt principle of similarity. Relations within the same unit are given more weight (they “belong” to the same perceptual entity), whereas relations assigned to different units are given smaller weights. Thus, two objects with different 3D shapes will contrast less than two objects having the same 3D shape. To test this proposal, Bruno et al. (2018) created a visual version of the Uznadze illusion. In each trial, they presented two inducing stimuli (a small and a large disk) side by side on a computer screen that flashed five times (i.e., the “inducing” phase), and then they were replaced with two intermediate disks, a standard and a test disk that varied from smaller to larger than the standard. Using the method of constant stimuli, Bruno et al. assessed points of subjective equality for the test

disks. Because these were always presented in the location of the large inducer, if there is a visual Uznadze illusion test disks having the same physical size as the standard should appear smaller than this standard. Thus, points of subjective equality should correspond to tests that are larger than the standard. This was the case: Visual judgments of the size were strongly depended on the Uznadze illusion. In addition, and in analogy to Kappers and Tiest (2014), Bruno et al. included incongruent inducing- induced pairs of stimuli to test whether similarity modulated contrast. They tested several features such as shape, orientation, and color. Their findings were similar to those found in Kappers and Bergmann-Tiest's work: The size contrast decreased for incongruent inducing-induced pairs stimuli, in comparison to the equivalent conditions where those features were the same. They interpreted their results as evidence that visual similarity modulates the gain of the size contrast signal within the visual system.

Given these results, it is interesting to ask whether the Uznadze illusion also affects motor responses. First, since the Uznadze illusion is a form of size contrast, it can be used to test the grasping-perception dissociation predicted by the TVSH within the same logic that has governed grasping studies with the Ebbinghaus illusion. In addition, by manipulating features in the inducing and induced stimuli, it is possible to investigate whether similarity affects the size representation used by the motor system. Last, the Uznadze illusion is a good candidate to test the TVSH for another less-obvious aspect. As briefly explained in the introduction section, the TVSH predicts that vision-for-perception holds information in memory for a relatively long time, whereas vision-for-action holds it only for a very brief time as action parameters need to be continuously updated. Thus, one would predict that dorsal processing should be relatively unaffected by contextual objects that were presented in the near past. In the Uznadze illusion, this is exactly what happens. Perceived size for a current target is affected by the size of another, contextual object that was presented slightly earlier. We sought to determine if a similar effect of temporal context could be detected for motor-related size

representations, as detailed in the following section. Finally, given previous results on the effect of similarity on the size of the Uznadze illusion in vision-for-perception (Bruno et al. 2018), it is also of interest to investigate if a similar modulation takes place in vision-for-action. This is another potential dissociation in the behavior of the two subsystems that, to the best of our knowledge, has never been tested before despite its obvious relevance to the functional interpretation of the two streams.

Rationale and specific objectives of the study

The above-listed considerations motivated our study. To investigate whether grasping is affected by the Uznadze illusion, we used a visual equivalent of Uznadze's haptic stimuli. In previous studies using the haptic and visual versions, inducing and induced stimuli were presented in pairs; in contrast, we displayed only one inducing and induced stimulus at a time; this is the first study that investigated the Uznadze illusion using this mode of presentation. Specifically, we employed large or small 3D disks as inducer stimuli to be presented first, and intermediate-size 3D disks as target (induced) stimuli to be grasped (or cross-modally matched in the comparison "perceptual" task) after seeing the inducers. Given that the Uznadze illusion yields consistent perceptual effects in haptics (Kappers & Bergmann-Tiest, 2014) but also with visual shapes presented on a computer monitor (Bruno et al., 2018), it is reasonable to expect that cross-modal matches (i.e., "manual estimations") will also reveal a detectable size contrast illusion. We sought to investigate if a comparable size contrast effect can be detected in the maximum in-flight aperture of precision grips. Given that, according to the TVSH, spatial codes for action are relatively insensitive to the context and relatively short-lived, one would predict that this motor "read-out" of the internal representation of size computed within vision-for-action would be relatively immune from the Uznadze illusion. In addition, we included a condition with incongruent inducing-induced pairs stimuli to investigate whether stimulus similarity affected size representation during the exposure of the Uznadze illusion.

Finally, as adopted in many recent studies, in our experiment participants performed both the perceptual and motor tasks in an open-loop procedure (i.e., without visual information) to ensure that responses were made only on what has been visually processed before initiating the movement. We contend that this methodology represents a strong test of the dissociation predicted by the TVSH.

Methods

Participants

We recruited participants from the University of Parma community. All were right-handed, had normal or correct-to-normal vision, no history of neurological disease, and were unaware of the purpose of the study. All gave their informed consent prior to participation in the study. The sample size was determined based on a power analysis conducted by Kopiske et al. (2016) for grasping data using the Ebbinghaus illusion and on a-priori considerations about pilot observations. Based on typical effect sizes in the literature, Kopiske and collaborators estimated that a sample size of 33 participants is needed to achieve 80% statistical power with alpha = 0.05 in an Ebbinghaus illusion study. Given that pilot observations in our Uznadze grasping task revealed the possibility of observing extreme values (i.e., participants showing very large motor effects but small perceptual effects, or very large perceptual effect but small motor), and given that modelling the data might require excluding such outlier values, we decided to raise our sample size to a conservative total of 64 volunteers (35 females, age range 23–39).

Ethical approval

The study was performed in accordance with the ethical standards of the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki), with the ethical

standards of the Italian Board of Psychologists (see http://www.psy.it/codice_deontologico.html), as well as the Ethical Code for Psychological Research of Italian Psychological Society (see <http://www.aipass.org/node/26>). As the study did not involve clinical treatments or the use of biomedical equipment with clinical implications, approval from the Parma hospital ethics committee was ruled as unnecessary.

Tasks and conditions

We compared two tasks: An open-loop grasping task and an open-loop cross-modal size-matching task. In both, visual information was removed as soon the participant started the movement. Thus, both were performed based on what had been visually processed before initiating the movement. In the grasping task, participants were requested to pick up the disk in front of them and to place it on the table immediately to the right of its initial position. The dependent variable in this task was the maximum in-flight grip aperture between thumb and index, or MGA. In the matching task, participants were requested to raise their hand near their body and to indicate, by opening the finger and the thumb, how big the disk appeared to them visually. The dependent variable is thus the matching thumb-index aperture (this is sometimes called “manual estimation”, or ME, see Haffenden and Goodale, 1998). In contrast to the grasping task, we did not require participants to pick up the disk after performing the matches. By avoiding haptic feedback in the matching task, we rendered this task more comparable with that of the earlier study (Bruno et al., 2018) which revealed similarity effects on size contrast using a standard psychophysical method with computer-presented figures. At the same time, we introduced a potentially relevant difference between the matching and the grasping task. Our aim here, however, was not to perform a quantitative comparison between potential effects on perception and action, but to test how these two tasks respond to the similarity manipulation. For this reason, we privileged comparability of the current matching task with the earlier psychophysical data, which revealed the similarity effects for the first

time, over comparability across the two tasks. In addition, tasks were carried out in two different conditions. In the congruent condition ($N = 32$), the inducing stimuli were identical to the targets in shape, color, orientation and color of the support panel. In the incongruent condition ($N = 32$), the inducing stimuli were different from the targets in shape, color, orientation and color of the support panel. Details on this manipulation are provided in the next section.

Stimuli

All stimuli were custom-made wooden disks (height = 1 cm). The target stimuli were three white disks having slightly different diameters (45 mm, 40 mm, and 35 mm). We introduced this small variation in the size of the targets to avoid stereotyped responses by participants and to estimate the slope of the linear function relating the response variable to the physical size of the stimulus (see “Results” section). Presentation of the targets was preceded by the presentation of the inducing stimuli. These were either white disks (diameter = 120 mm, 40 mm, or 10 mm) mounted on a black rectangular panel (30×21 cm) or black squares having approximately the same area as the white disks (side = 105 mm, 35 mm, and 8 mm), mounted on a white panel (also 30×21 cm). Thus, in one condition the targets and the inducers were similar in shape and color (congruent condition); In another, they were different in shape and color (incongruent). The full stimulus set is presented in Fig. 2.1.

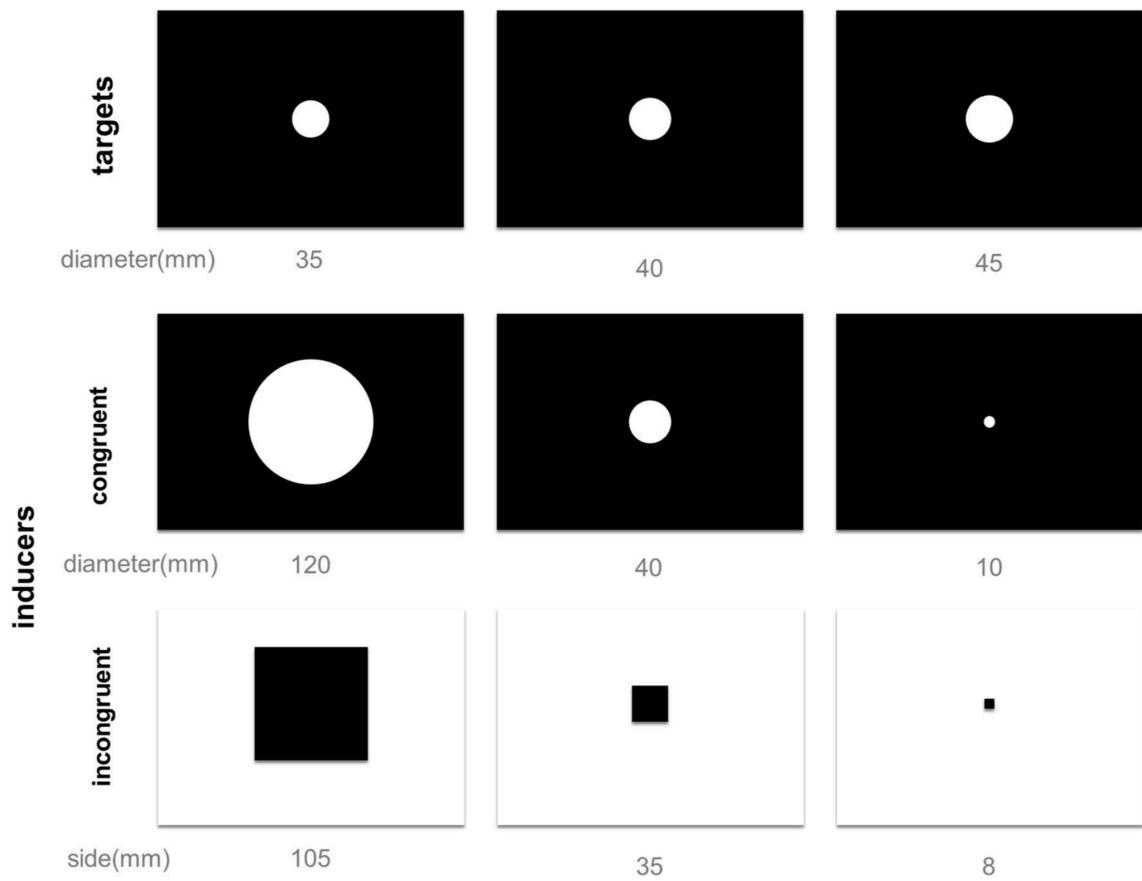


Fig. 2.1. Stimulus set. Upper panel: Target disks used in both conditions; Middle panel: Inducing disks used in the congruent conditions; Lower panel: Inducing squares used in the incongruent condition.

Apparatus

Participants sat on an adjustable chair in front of a rectangular table (90 × 80 cm). A keyboard was placed on the table in front of the participant, and a plastic support was mounted exactly 43 cm in front of the spacebar on this keyboard. Both the center of the support and the center of the spacebar were aligned with participant's midline. Background panels with inducing or induced stimuli were mounted on the plastic support in a quasi-vertical position. The plastic support allowed for rapid removal of the panels holding the inducers and for their immediate substitution with the panels holding the target disks. Visual feedback was removed using PLATO visual occlusion spectacles

(Translucent Technologies Inc., Toronto, Ontario, Canada—Milgram, 1987), which have a translucent-to-opaque latency of 3–4 ms. Response kinematics were recorded using a BTS-DX100 Smart System (sampling rate 100 Hz, spatial precision at least < 0.2 mm with four cameras at distances of 1–1.5 m from the participant’s hand) using three markers (one on the wrist, one on the tip of the index, and one on the tip of the thumb). A personal computer running Matlab R2011b under Windows 7 was used to control stimulus presentation and to manage trigger signals to the Plato spectacles and the BTS motion tracking system.

Design

The design resulted from crossing three within-participant independent variables and one between-participant independent variable. The within variables were the target and inducer sizes (three levels each, see the previous section) and the task (grasping and manual estimation), whereas the between variable was the congruency manipulation (congruent and incongruent). Each inducer stimulus was presented 15 times (five times at each target size), resulting in 45 trials in the grasping task and 45 trials in the manual estimation task in each congruence group. Each participant performed the two tasks in two separate blocks which were counterbalanced across participants. Inducer and target diameters were randomized within each block. The dependent variable was a measure of the index–thumb aperture, taken in the manner appropriate to the task. In the grasping task, this was the maximum in-flight grip aperture (MGA) between the thumb and index during the grasping movement. In the manual estimation task, this was the aperture of the thumb and index as shown by the participants to match the disk diameter (ME).

Procedure

Each block began with a brief verbal and motor explanation of the task, followed by some practice trials using randomly chosen inducers and targets.

Trial structure in both tasks is schematized in Fig. 2.2. The procedure for each task was the same until the last part. At the beginning of each trial, the shutter spectacles were turned off (opaque). The participant waited for a go signal from the experimenter while keeping his or her thumb and index in a pincher position on the spacebar. The experimenter read off the inducer–target pair for the current trial from the computer screen, placed the appropriate inducer stimulus on the support in front of the participant, and verbally gave the go signal. At this point, the participant pressed the spacebar to start the inducer phase: That caused the spectacles to turn on (transparent) and off (opaque). Opening and closing of the spectacles were both repeated five times, each of 250 ms, for a total induction time of 2.5 s. During this sequence, participants were asked only to observe the inducer stimulus placed on the support in front of him. At the end of this sequence, the spectacles remained closed and a sound from the speakers informed the experimenter to substitute the inducer stimulus with the target. This substitution was executed by first manually removing the panel with the inducer stimulus, then placing the second panel with the target stimulus. This operation required about 2 s, on the average. Once the target disk was placed in the appropriate position, the experimenter verbally gave a second go signal. The participant pressed the space-bar again, but this time he or she was requested to hold it down as long as needed to observe the target stimulus (the spectacles turned opened and remained transparent as long the participant held the spacebar down). From now on, there were some slight differences in the procedure between the tasks. In the grasping task, the button release turned off the spectacles and triggered the kinematics recording; The system recorded for 3 s, giving the participant ample time to grasp the target stimulus, lift it on the table, and complete the trial. In the manual estimation task, the button release did not trigger the kinematics recording but just turned off the spectacles. The participant performed the match by opening index and thumb as deemed appropriate, then pressed one other button with the left hand to record the response. This second button press triggered the kinematics recording for

only 0.1 s to measure the fingers' aperture. The participant brought his hand back in the start position at the end of the trial, waiting for the go signal of the next trial. If an error occurred for whatever reason, the experimenter noted the details of the relevant trial. All trials classified as errors were repeated in random order at the end of each block.

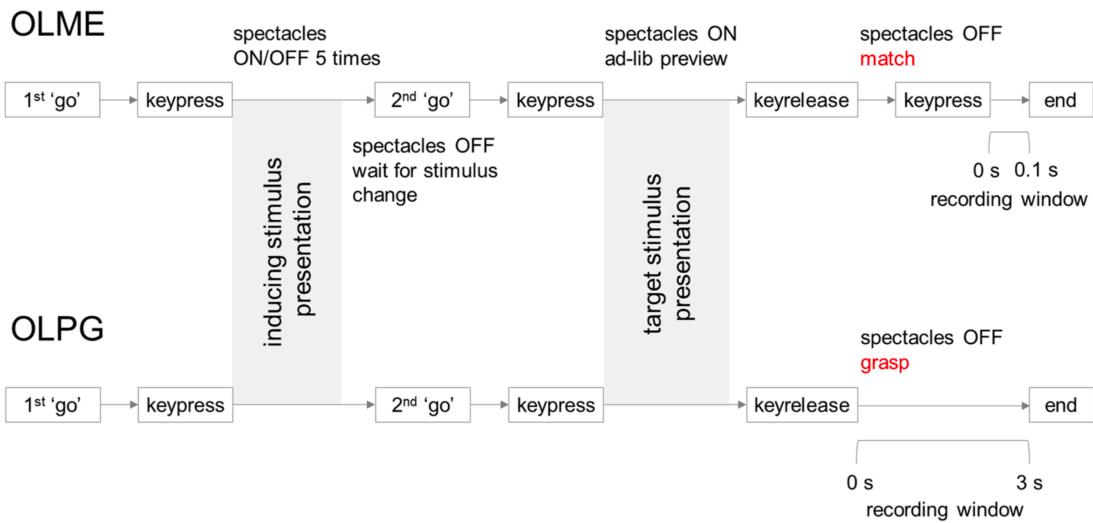


Fig. 2.2. Trial structure in the two tasks: Open-loop precision grip and open-loop manual estimation.

Data validation and analysis

To screen for atypical grasping profiles, records of all trials were inspected off-line by two of the authors (S.U. and V.P.). All trials that met the following three criteria were considered as correct: (1) the distance between the thumb and the index markers at the beginning of the movement was 2 ± 0.1 cm (given the position of the markers, this corresponded to thumb and index touching); (2) the plot of inter-marker distance as a function of time exhibited a smooth and rapid growth and a single unambiguous peak, followed by a slower decrease back to the initial offset (for an example, see Fig. 2.3); (3) the value of the peak of the maximum grip aperture or MGA was no greater than 15 cm (chosen based on informal assessments of MGA ranges in different

individuals and on an assessment of the constant positive error due to the marker positions). Trials classified as incorrect were discarded before analysis. Data validation according to these criteria resulted in the exclusion of 0.5% of all trials from all participants.

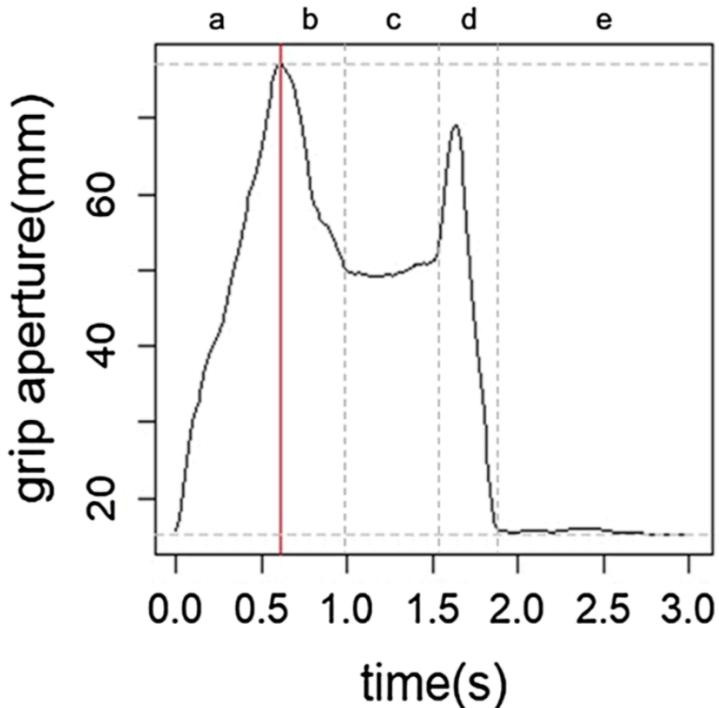


Fig. 2.3. Thumb-index aperture as a function of time in a representative trial. a) Approach and opening phase; b) Max aperture and closing phase; c) Stable grip while moving the disk; d) Release; e) Return to start position.

Once all trials were checked, all recordings were further analyzed to compute the max grip apertures (grasping task) and finger apertures (manual estimation task) data. These parameters were computed by means of R scripts which allowed visualizing finger trajectory, velocity, and fingers aperture as a function of time. The distance between thumb and index of manual estimations and grip apertures were computed as Euclidean distances between two points in the space. Given that grasping and manual estimation tasks yield different psychophysical functions, however, finger

aperture data are not directly comparable in these two tasks (see Bruno & Franz, 2009; Franz 2003; Kopiske et al., 2016). Manual estimation apertures closely correspond to actual widths, yielding linear functions with unitary slopes and minimal intercepts. Instead, grasping MGAs yield linear functions with slopes around only 80% of the actual width, and large intercepts (see Smeets and Brenner 1999). To take this difference into account, it has become customary to adjust the raw aperture data by the appropriate slope and to express it as a percentage of physical size. Accordingly, for each task, we calculated a percent corrected illusion effect using the formula proposed by Bruno and Franz (2009):

% corrected effect =

(expanding raw effect – compressing raw effect) / slope × true width × 100,

where expanding and compressing effects refer to the size-contrast due, respectively, to the small inducing disk and the large inducing disk, true width is the actual width of the target disk, and slope refers to the slope of the linear function describing the scaling of the employed measure to actual width (i.e., in the grasping or manual estimation task).

Results

Overall distributions of ME and MGA

Figure 2.4 presents the overall distributions of the maximum grip apertures in the grasping task (MGA) and of the manual estimations (ME) in the matching task. In the MGA distribution ($N = 2862$), the group average was 75.64 mm; skewness and kurtosis were, respectively, 0.07 and 4.71. In the ME distribution ($N = 2873$), the group average was 55.84 mm; skewness and kurtosis were, respectively, 0.44 and 4.17. Thus, both distributions were essentially symmetric and reasonably similar to a normal distribution.

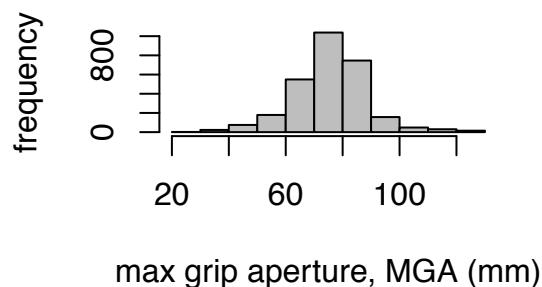
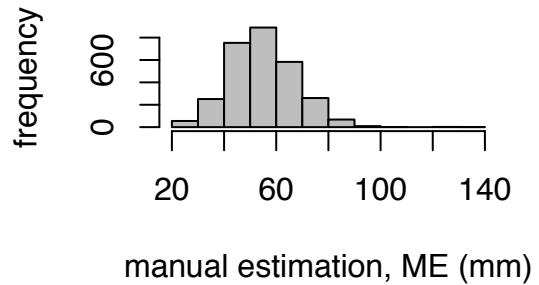


Fig. 2.4. Overall distributions of manual estimations (ME) and the maximum grip apertures (MGA).

Figure 2.5 presents the aperture data as a function of the physical size of the target disk. We display arithmetic mean apertures for each participant in each task, target levels, and condition, as well as group averages for the same factors. In both tasks, finger apertures were an approximately linear function of the disk's size. Thus, we fitted a linear model for each participant predicting finger apertures as a function of target diameters and computed mean slopes by averaging individual slopes in each of the four cells of our design (grasping congruent, manual estimation congruent, grasping incongruent, and manual estimation incongruent). Interval estimates (confidence level = 0.95) of slopes and intercepts were, respectively, 0.89 ± 0.13 mm/mm and 69.78 ± 2.53 mm for the grasping congruent task; 1.01 ± 0.158 mm/mm and 48.38 ± 2.05 mm for the manual estimation congruent task; 0.95 ± 0.13 mm/mm and 71.44 ± 2.01 mm for the grasping incongruent task; 1.22 ± 0.16 mm/mm and 49.14 ± 2.08 mm for the manual estimation incongruent task.

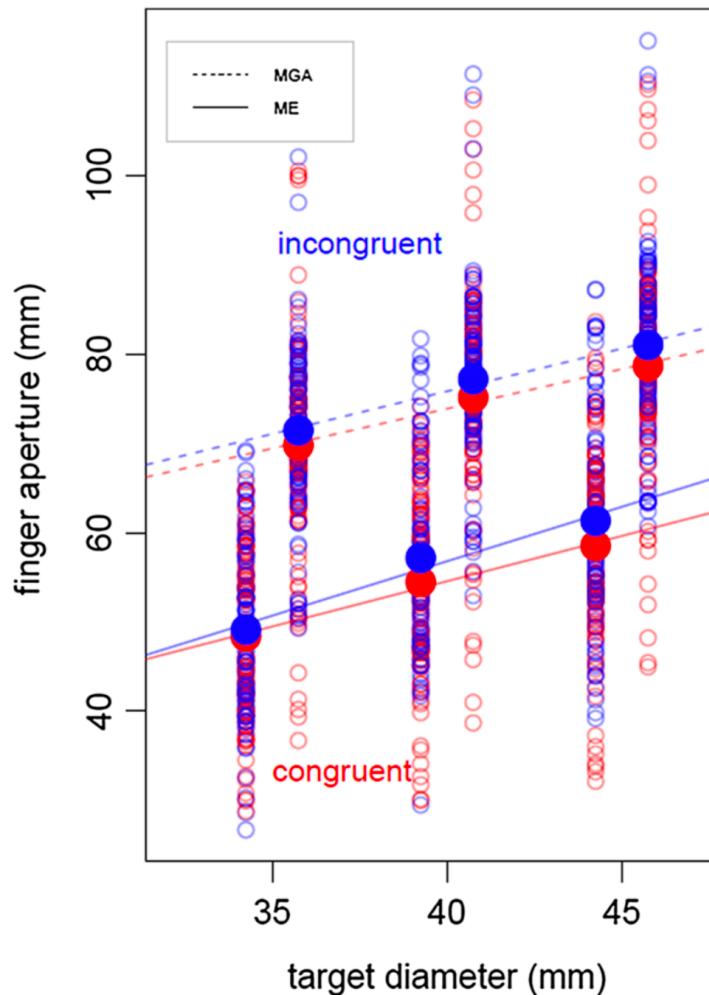


Fig. 2.5. Mean finger apertures as a function of target disk size, task (grasping vs. manual estimation) and congruency (red, congruent; blue, incongruent). Open circles: Individual means. Filled circles: Group averages. Solid lines: Linear regressions for the manual estimation task; Dotted lines: Linear regressions for grasping task.

Figure 2.6 presents finger apertures as a function of the inducer size. For simplicity, we considered the three levels of the target disk (35, 40, and 45 mm) as if they were a one-level factor. This is justifiable if we assume that the average of apertures performed with the 35 mm disk and the 45 mm disk is the same as the average of the intermediate disk apertures. This assumption

is equivalent to assuming that finger apertures are a linear function of target size (see again Fig. 2.5). In our dataset, the actual grand averages of finger apertures when the target was 40 mm vs. 35 mm or 45 mm were 65.9 mm and 64.8 mm, respectively. The slight difference may be taken as an indication that linearity is not perfect at least in this dataset.

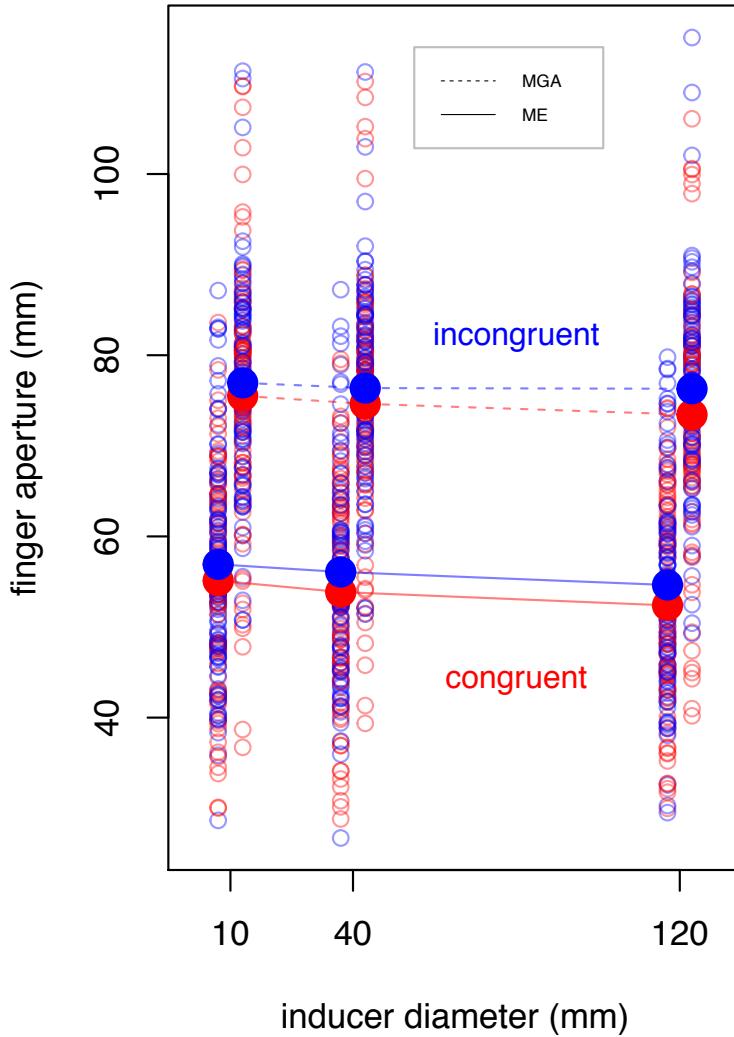


Fig. 2.6. Mean finger apertures as a function of inducer stimulus size in the grasping and manual estimation tasks (congruency: Congruent in red, incongruent in blue). Lines describe the finger aperture trend across inducing stimuli. All plotting conventions in Fig. 2.5.

As in the previous plot, we display arithmetic means for each participant in each task, inducer levels, and condition as well as group averages. The plotted lines represent the finger aperture trend. Mean values and standard

errors are reported in detail in Table 2.1. As can be seen in this table, data from the congruent condition support an effect of the Uznadze illusion in both tasks. Relative to baseline (i.e., when inducer and target diameter were of the same size) mean finger apertures in this condition consistently increased when the target disk was preceded by the smaller inducing stimulus and decreased when the target was preceded by the larger inducing stimulus. Data from the incongruent condition, conversely, reveal a somewhat different pattern. Relative to baseline, means in the perceptual task remain smaller with the large inducer and larger with the small inducer. This pattern is therefore again consistent with the Uznadze illusion. However, the size of the differences is now much smaller than in the congruent condition. Means in the motor task, conversely, do not show a pattern consistent with the Uznadze illusion. Relative to baseline, the mean aperture following a smaller inducer is smaller, not larger as one would predict based on the illusion effect, although this difference is also rather small. The mean aperture after a larger inducer is essentially identical to the baseline.

Task	Congruence	Inducer size (mm)	Finger aperture group averages (mm)	Sem
ME	Yes	10	55.12	1.38
ME	Yes	40	53.86	1.40
ME	Yes	120	52.39	1.33
MGA	Yes	10	75.51	1.66
MGA	Yes	40	74.63	1.61
MGA	Yes	120	73.43	1.58
ME	No	10	56.92	1.49
ME	No	40	56.06	1.42
ME	No	120	54.62	1.39
MGA	No	10	75.51	1.36
MGA	No	42	76.36	1.28
MGA	No	120	76.31	1.35

Table 2.1. Average group finger apertures, with group (across participant) standard errors, as a function of inducer size, task (grasping–manual estimation), and congruency (congruent–incongruent). The size parameter refers to the diameter of an actual inducer disk (congruent condition) or to the diameter of the circle that would have the same area as the inducer square (incongruent condition). See text for details.

At least qualitatively, means presented in Table 2.1 are consistent with the previous observations by Bruno et al. (2018). When the inducing initial object was identical to the induced object, the pattern is what one would expect if there were a robust size contrast effect in both the perceptual and the motor task, that is, if the Uznadze illusion did affect grasping as well as manual estimation responses. However, the size contrast effect is reduced when the inducing initial object was different (in color and shape) from the induced object. The reduction is strong in the perceptual task, and even stronger (to the point that the contrast effect seems to disappear, at least as measured by these averages) in the motor task. Before presenting an interpretation of these findings, we note, however, two things. First, the data plotted in Fig. 2.6 and summarized by the statistics in Table 2.1 refer to the complete, raw aperture data, and suggest substantial individual differences in the performance of our participants. Second, aperture data from grasping (i.e., MGA) and from matching (ME) are not immediately comparable for the reasons detailed in the section on Data Validation and Analysis above. For these reasons, we reanalyzed the data after computing an overall percent correct illusion effect for each participant in each task, as detailed in the preceding section, and after performing outlier identification to exclude participants that could distort the overall trend.

Percent corrected illusion effects

Figure 2.7 presents the percent corrected illusion effects in the grasping and manual estimation tasks for each participant. Corrected effects were computed using the formula adopted by Bruno and Franz (2009, see “Data validation and analysis” section), for each participant for both tasks, yielding 32 corrected effects for each group (grasping congruent, manual estimation congruent, grasping incongruent, and manual estimation incongruent) for a total of 128 percent corrected effects.

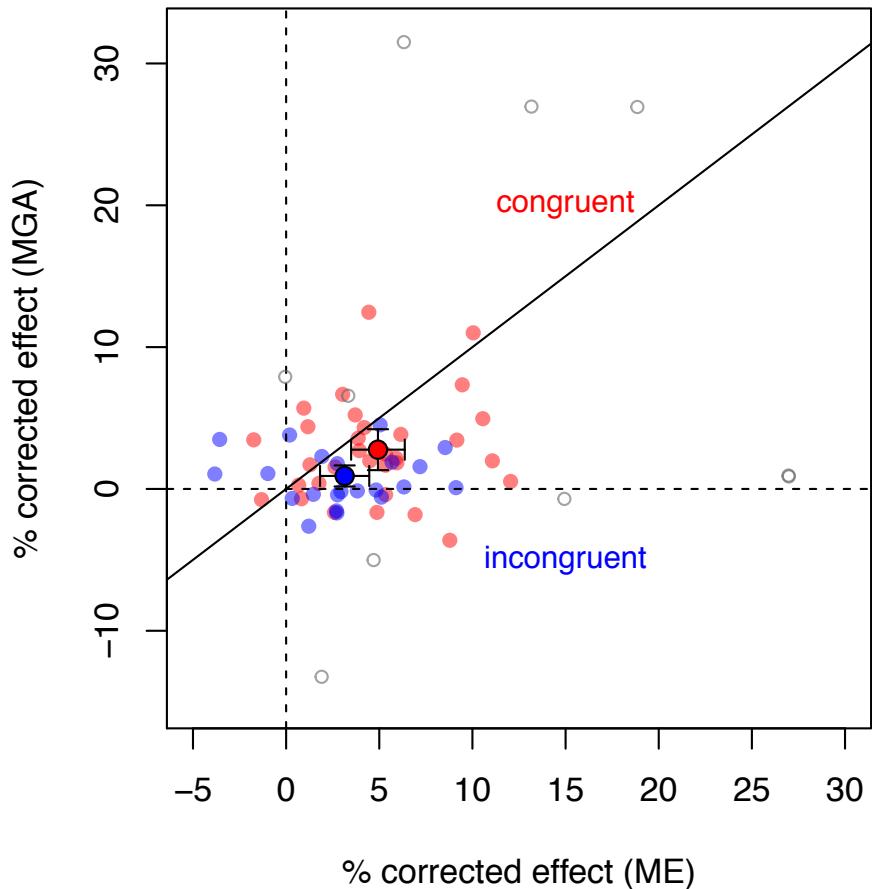


Fig. 2.7. Percent corrected effects in the grasping (MGA) and matching (ME) tasks, as a function of congruence (red = congruent, blue = incongruent). Dashed gray lines: Expected result if corrected effects are zero in the grasping (horizontal) or matching (vertical) tasks. Diagonal solid line: Expected result if corrected effects are the same in the two tasks. Shaded circles: Individual effects in each participant. Gray empty circles: Outliers (these were excluded before fitting a linear model). Contoured circles: Group averages. Error bars: 99% confidence intervals as recommended by Loftus and Masson (1994) for within-participant designs.

Before proceeding further, we tested for extreme values that could affect the overall trend of the corrected effects. To assess this, we used the algorithm for robust outlier detection recommended by Leys et al. (2013):

$$\text{abs(individual effect - MEDIAN)} / \text{MAD} > 3,$$

where abs signifies the absolute value of what follows in parenthesis, MEDIAN is the median of the distribution of the appropriate corrected effects distribution (grasping congruent, manual estimation congruent, grasping incongruent, and manual estimation incongruent), and MAD is the median absolute deviation of the appropriate distribution. We detected 10 outliers by this criterion (3 grasping congruent effects, 1 manual estimation congruent effect, 4 grasping incongruent effects, and 2 manual estimation incongruent effects). Since each participant had one motor and one perceptual effect, the respective effect associated to the outlier value was also excluded from the analysis. Hence, a total of 10 participants were excluded from this analysis. Percent corrected average effects (and associated standard errors) were $2.77 \pm 0.7\%$ for the grasping congruent task; $4.92 \pm 0.7\%$ for the manual estimation congruent task; $0.91 \pm 0.36\%$ for the grasping incongruent task and $3.14 \pm 0.64\%$ for the manual estimation incongruent task. An analysis of variance testing differences in finger aperture as a function of task (grasping, manual estimation), congruence, and their interaction revealed significant effects of both predictors (task, $F(1, 52) = 13.5$, $p < 0.05$; congruence, $F(1, 52) = 7.74$, $p < 0.05$), whereas the task \times congruency interaction failed to reach statistical significance ($F(1, 52) = 0.002$, $p = 0.96$).

Discussion

The action-perception dissociation proposed by the TVSH led to the counterintuitive prediction that actions should resist visual illusions. However, it remains controversial whether perception and action can be dissociated in the context of illusions and what are the implications for the TVSH. Here, we provided data about the unexplored Uznadze illusion as a better candidate to test the dissociation. The main findings are discussed below.

The Uznadze illusion affects both vision-for-action and vision-for-perception

The first purpose of this study was to test whether the Uznadze illusion affects finger apertures during a motor and a perceptual task. Figure 2.6 shows that mean finger apertures in both tasks increased when the target disk was presented after seeing the small inducing disk and decreased when the target disk was presented after seeing the large inducing disk. This trend is consistent with previous assessments of the Uznadze illusion in haptics (Kappers & Bergmann-Tiest, 2014) and vision (Bruno et al., 2018). At this first step of analyses on the raw data, it is already possible to support that both grasping and manual estimation responses were sensitive to this type of sequential contrast. Although this average difference is already evident in the raw data, however, it is partly masked by individual differences in psychophysical functions between the two tasks. Indeed, as expected, in both our tasks, finger apertures were linearly scaled to the disk size, but with different slopes. The average slope for the manual estimation task was above 1.0, while for the grasping task was below 1.0; these values are consistent with previous estimates (see Smeets & Brenner; 1999) and suggest that our two tasks tapped on the same processes as previous illusion studies. Thus, a slope correction was needed to evaluate the size contrast effect on grasping and manual estimation outcomes. In Fig. 2.7, we reported the per cent corrected effects of each participant computed adopting the correction formula proposed by Bruno and Franz (2009). Lower limits of interval estimates are consistent with the conclusion that all averages for these effects are different from zero in all four groups. Thus, these results support that both vision-for-action and vision-for-perception were clearly affected by the Uznadze sequential contrast.

Stimulus similarity affects both vision-for-action and vision-for-perception in a comparable way

The second purpose of the present study was to investigate whether stimulus similarity modulates the size representation during the exposure of the Uznadze illusion. In both motor and perceptual tasks, corrected effects decreased with incongruent pair stimuli in comparison to the congruent condition. Once again, these findings are in accord with the analogous results found in the haptic version of Kappers and Bergmann-Tiest (2014) and in the visual version of Bruno et al. (2018). According to the TVSH, given that vision-for-action uses effector-relative frames of reference for guiding actions, size representation should be relatively unaffected by contextual cues. Our results do not support this prediction, in contrast to the TVSH, vision-for-action proves sensitive to a global property of the context such as the similarity between two objects. An issue that remains unresolved with this respect is whether it was similar in shape or in color, or both, that determined the modulation. In the study of Bruno et al. (2018), shape and color (as well as color and orientation) were manipulated individually and all proved effective as dimensions of similarity that provoke the effect. In the current study, however, it is not logically possible because we manipulated similarity along two different features at the same time (shape and lightness). We did this because this was our first attempt to test the similarity effect on action and we want to create strongly incongruent inducing and target stimuli to maximize our chances of detecting it. Further research is needed to determine if vision for action responds to the same dimensions of similarity that have been shown to be effective to modulate the effect in vision for perception. Results of such study may even reveal an unexpected dissociation between the two functional systems.

Vision-for-action is sensitive to temporal context

Before concluding, it is necessary to discuss a critical aspect of the procedure we adopted. In Bruno et al.'s work, the time lapse between the inducer offset and the target onset was immediate, due to the stimuli presentation on a

computer screen. In contrast, with real 3D objects, manually swapping the inducing and induced stimuli necessarily requires a certain amount of time. In the present study, the experimenters were well trained to substitute the inducing disk with the target disk as fast as they could. Still, on average, we estimate that the substitution required around 2 s. This was, therefore, an unavoidable interstimulus interval that affected all trials. In addition, consider that the presentation of the induced test stimuli was not immediately after the swap and required the participant to react to the go signal and press a key to open the shutter glasses. In accord to the TVSH, the dorsal stream possesses a short-lived memory as spatial parameters can be continually checked online during the actual movement. If this was true, one would expect that a rather conspicuous delay between the inducing and induced stimuli should greatly limit the effect of the Uznadze illusion on finger apertures during the grasping task. In contrast, our results clearly showed that grasping was affected by the sequential contrast although the stimuli substitution caused a remarkable delay in the presentation of the second test stimulus. At least in this specific aspect, therefore, the vision-for-action system proves to be quite sensitive to the temporal context and to possess a certain ability to maintain information in memory. We suggest therefore that this also is evidence against the TVSH.

Conclusion

The Uznadze illusion is a clear demonstration that size perception strongly depends on a comparison with the previously presented context, both in the haptic and vision systems. In this paper, we have shown that a version with 3D objects of the Uznadze illusion can be realized to test the action-perception dissociation. This is the first study to report the influence of the Uznadze illusion on grasping. We observed that the Uznadze illusion affected perceptual and motor responses in a similar way. Furthermore, stimulus similarity affected the size representation in both tasks in a comparable way,

suggesting once again that both vision-for-action and vision-for-perception operate with the same global contextual information. These results provide new evidence that a complete dissociation between perception and action as predicted by the TVSH is no longer supportable.

Chapter 3

The Uznadze illusion reveals a two-pronged dissociation between perception and action

Manuscript in preparation as: Bruno, N., & Uccelli, S. The Uznadze illusion reveals a two-pronged dissociation between perception and action. Draft wrote by Stefano Uccelli for the present dissertation.

Abstract

In daily life, it is essential to obtain information about the size of objects for grasping them. We may obtain an accurate size representation either from vision or haptics, but it is unclear how prior visual or haptic information of an object affects the size representation for an upcoming visuomotor process for a different object. We tackled this issue by using the Uznadze illusion, in which the same ‘test’ object appears smaller (or larger) after the exposure of a larger (or smaller) ‘inducing’ object. Participants grasped (motor task) a test ball and then provided a match of its size (perceptual task) after having either inspected visually or explored haptically a large or a small inducer ball, either presented in the same or a different position relative to the test. Surprisingly, motor, but not perceptual, responses revealed size contrast (the Uznadze illusion), or size assimilation (the inverse Uznadze illusion), or even no illusion, depending on which sensory channel and spatial position the inducer was presented. Thus, this study reveals a two-pronged dissociation that seems based on factors related to multisensory integration and the internal schema of the hand rather than distinct size representations between perception and action.

Introduction

We retrieve information about objects by merely observing them. Such knowledge relies predominantly on visual information, which is essential to recognize object features such as size, shape, orientation, and color. And among these, size is vital to interact with objects in daily life. When performing actions such as, for instance, grasping an object, the visual system creates an internal representation of the object size to guide the hand and perform the grasp successfully. However, we may get also an idea of an object size by simply exploring its surface with the hand. The activation of mechanoreceptors and stretch receptors during active touch (haptics) provide rich information about object structure (Gibson, 1962), including its size. It is known that both vision and haptics provide estimates of an object size rather accurately (Ernst & Bulthoff, 2004; Ernst & Banks, 2002). It is poorly known, however, how prior visual or haptics information relates to an upcoming visuomotor process. The present work aims to investigate whether previous information acquired from visual or haptics channels has a different impact on the size representation for grasping an object.

When looking at an object, size is retrieved in cortical visual areas by coding visual information entering the eye. Such internal representation promotes constancy under changes in viewing conditions to promote recognition of objects (Biederman, 1987; Marr, 1982). At present, however, it is partially unclear how visual information is used by the motor system for preparing a visuomotor process. Specifically, a longstanding debate in the cognitive neurosciences concerns how size representation is coded for guiding actions such as grasping. According to the two-visual-systems-hypothesis (TVSH, Milner & Goodale, 2008, 2006, 1995), size representations are coded in critically different ways in the dorsal and ventral streams (also called vision-for-action and vision-for-perception, respectively). These key differences in turn have several behavioural consequences. In particular, the TVSH predicts

a relative immunity of the dorsal representations of size from stimulus-contextual effects (e.g., visual illusions) such as those observed routinely for consciously perceived size. This prediction is also supported by the online view of motor control encapsulated in the TVSH, (Westwood & Goodale, 2003) which states that dorsal representations decay immediately as they are continuously updated for supplying the ongoing action. Although the TVSH represents a landmark in cognitive neuroscience on visuomotor processing, a massive amount of controversial evidence has been collected in the last decades (for instance Grünbaum, 2018; Schenk & Hesse, 2018; Rossetti, Pisella, & McIntosh, 2017; Schenk & McIntosh, 2010).

The predictions of the TVSH have been challenged by a study of our group (Uccelli, Pisu, Riggio, & Bruno, 2019) which investigated a visual version of Uznadze illusion in action. In this illusion, the same ‘test’ object appears smaller (or larger) after the exposure of a larger (or smaller) ‘inducing’ object (Uznadze, 1966). That is, this temporal context induces a size contrast in perceiving the size of the induced stimulus. In Uccelli et al.’s work (2019), participants grasped (motor task) a test object or provided a match of its size (perceptual task) after the exposure to larger or smaller inducing stimuli. Two measures were compared: The maximum grip aperture (MGA) and the manual estimation (ME). The former consists of the max index-thumb distance reached during the in-flight grasping movement and represents a marker of the size representation computed by visual information for guiding grasps (Marteniuk et al., 1990; Jeannerod, 1981). The latter consists of a manual report made by distancing the thumb and index finger matching the perceived size (see Haffenden & Goodale, 1998). For both MGA and ME data, results revealed that finger apertures show a shrinking or an enlarging effect due to the Uznadze size contrast. The authors claimed that size representations in action and perception do not differ with each other and both rely on previous contextual information.

The aforementioned study revealed that previous visual information affected the size representation of successive visuomotor processes (i.e., the grasp). That is, it consisted of a two-sensory interaction. Whether previous haptics information has a similar influence represents an interesting, and largely unexplored three-sensory interaction. Since the Uznadze illusion has revealed strong size-contrast effects in haptics (Daneyko, Maravita, & Zavagno, 2020; Kappers & Bergmann-Tiest, 2014), previous information acquired haptically may have an effect on the size representation for a later visuomotor program. In haptics, size is presumably coded based on an internal body schema. Haptic estimates of an object size depend on afferences from skin mechanoreceptors combined with proprioceptive inputs signaling the interdigit distance (Berryman, Yau, & Hsaio, 2006), which they need tot be combined with an internal model of the hand (Allen, Michaelman, & Roberts, 1989; Klatzky & Lederman, 1993). The idea of an internal schema of the hand is not new, and comes from studies on the fake hand illusion (Tsakiris & Haggard, 2005; Botvinick & Cohen, 1998), in which synchronous multisensory signals can induce a (temporary) reorganization of the internal hand model, creating the illusion that a fake hand has somehow become one's hand (see Makin, Holmes, & Ehrsson, 2008). For instance, Bruno and Bertamini (2010) induced participants with fake hands smaller or larger than the participant's hand. Then, participants received a 'standard' disk in one hand, and a 'test' disk in the other hand, and felt actively the test disk sizes with the thumb and index fingers. Participants overestimated (or underestimated) the test size after exposure to the large (or small) fake hand. Therefore, this short multisensory stimulation altered the internal hand scheme which in turn affected the estimation of the test size.

At present, however, it remains partially unclear whether a modification of the hand scheme affects size representation in grasping. For instance, exposing participants to an enlarged visual version of their hand decreases the MGA for grasping an object (Bernardi et al., 2013; Marino et al., 2010). However, the

opposite case (i.e., viewing a shrunken hand) did not increase the MGA (see also Pavani & Zampini, 2007 for similar results with a pointing task). Bruno and Bertamini (2010), in contrast, found that inducing participants with large fake hands revealed overestimation of object size, i.e. the opposite outcome of Marino et al. (2010). Testing whether the hand scheme affects size representation in grasping would be easy with the Uznadze contrast by asking participants to explore haptically the surface of large or small objects and then grasp a different object.

Last, we introduce one other aspect not tested yet. Usually, the Uznadze illusion has been studied by presenting the inducing-induced pair of stimuli in the same spatial position. In haptics (Kappers & Bergman-Tiest, 2014) this was the same hand, in vision (Bruno et al., 2018) the same computer screen coordinates, and in grasping (Uccelli et al., 2019) the same spatial location. But what would happen if the two stimuli are presented in incongruent spatial positions? All the three mentioned studies above reported that the Uznadze illusion decreases when the pair of stimuli differed in their features (e.g., different shapes and/or colors). Therefore, a plausible expectation for presenting stimuli in incongruent spatial positions is to observe weaker (or maybe null) effects. This may be tested easily by presenting participants with inducers in a different position relative to the test.

Given the considerations above, we outline our objectives. To help the reader understand our experimental setup, imagine the following scene. You are sitting at your desk, and in front of you are a rubber ball of medium size and a larger baseball. At first, your job is to get an idea of the baseball size. You may merely observe the baseball, but you may also explore it by touching its surface with the tips of your index and thumb fingers; In both cases, your brain acquires information about the object size. Suppose now that you have to grasp the medium rubber ball. According to Uccelli et al. (2019), previous visual information about the baseball size will shrink the finger aperture for grasping the rubber ball (i.e., the Uznadze effect). But having acquired haptic

instead of visual information would return the same outcome? And would this depend on whether the two balls share or not the same spatial position? These are intriguing research questions that might reveal new insights on how action and perception represent the size of objects. In the next section, we present in detail the experimental paradigm and results. Then, we critically discuss these findings within the debate on the action-perception dissociation.

Methods

Participants

Ten participants were tested (4 females, mean age: 30.5; range: 24 - 58). They were the authors (N.B. and S.U.) and 8 volunteers who were naïve to the aims of the study. We chose to test a restricted sample of participants as the haptic size-contrast effect that formed the starting point for the study (the Uznadze illusion) is a well-understood, extremely robust phenomenon that can be readily demonstrated to anyone with essentially no individual differences. We therefore expected to observe it in the relevant experimental condition for all participants, and to use it as a baseline for comparison in the other conditions within and between participants.

Stimuli

We used three commonly commercially available balls: A regulation baseball (large, diameter \approx 70 mm), a rubber toy ball (medium, 45 mm), and a marble (small, 15 mm). The top left of Figure 3.1 displays these three stimuli. All three were used as inducing stimuli, whereas only the medium ball was used as a test stimulus. Thus, exposure to a large inducer yielded a successive contrast that was expected to reduce the perceived size of the test; exposure to a small inducer yielded a contrast expected to enlarge its perceived size; and

exposure to a medium inducer generated a baseline no-contrast condition for comparison.

Task

Participants were requested to reach and grasp the test ball and place it on the table ~10 cm to the right of its original position. Participants used the index and thumb of the right hand, which was the same hand that had been exposed to the haptic inducer (see next section). Once grasped the test, participants also added two finger contacts with the ball after they had placed it on the table. Finally, participants provided a match to the perceived size of the test ball by adjusting the aperture of their left hand index and thumb fingers. The match was always performed while the right hand index and thumb were still touching the test ball. Both the grasping and the matching responses were performed in full open-loop conditions by means of shutter glasses. Specifically, participants could visually inspect the test ball they had to grasp for as long as they wished, but as soon they lifted their hand to reach for it, the glasses closed and everything else was done without visual feedback.

Experimental conditions

All participants performed the task in four conditions. The inducing balls were presented either haptically or visually. In the former, participants explored the inducing ball by moving the right thumb and index fingers slightly around the surface (i.e., a ‘contour following’ exploratory procedure, see Lederman & Klatzy, 1987) without having visual information available (‘haptic inducing’). In the latter, participant merely observed the inducing ball through the shutter glasses’ lens over the exposure length (‘visual inducing’). The inducing balls were presented on the table either in the same position of the test ball (‘spatially congruent’) or in a different position (‘spatially incongruent’). Thus,

by crossing these two manipulations yielded four experimental conditions that from now on will be referred as to ‘haptic congruent’, ‘haptic incongruent’, ‘visual congruent’, and ‘visual incongruent’ conditions.

Apparatus

Participants sat on an adjustable chair in front of a rectangular table (90 × 80 cm). Two faint cross-marks drawn on the table marked the position of the inducing and test balls. In all conditions, the test ball was placed on the cross-mark positioned at 40 cm from the spacebar (~ 43 cm from the edge of the table); both the cross-mark and the center of the spacebar were aligned with the participant’s midline. The inducing balls’ position was different between congruent and incongruent spatial conditions: In the former, inducing balls were placed on the same cross-mark of the test; In the latter, they were placed on the cross-mark to the right of the participant at 10 cm from the right edge of the table (~ 35 cm from the spacebar). An exception was the visual incongruent condition in which the area of the table was extended by posing a larger panel on it. The purpose was to present participants with the inducing balls in a larger visual field devoid of external references that could interfere during the visual induction. Top right panel of Figure 3.1 depicts the experimental apparatus.

Visual feedback was removed using PLATO shutter glasses (Translucent Technologies Inc., Toronto, Ontario, Canada), which have a transparent-to-opaque latency of 3-4 ms. Kinematics were recorded using a BTS-DX100 Smart System (sampling rate 100 Hz, spatial precision at least < 0.2 mm with four cameras at distances of 1–1.5 m from the participant’s hand). Three markers were placed on the wrist, the tip of the index, and the tip of the thumb of the right hand; two additional markers were placed on the tips on the index and thumb of the left hand. A personal computer running MATLAB (2013b, The MathWorks, Natick, MA, USA) under Windows 7 was used to control

stimulus presentation and to issue trigger signals to the glasses and the tracking system.

Procedure

The experiment began with a verbal explanation followed by 6 practice trials with randomly chosen inducers. Participants then performed the experimental trials. Trial structure is schematized in the middle and bottom panels of Figure 3.1. At the beginning of each trial, the shutter glasses were turned off (opaque). The MATLAB program running the experiment presented the trial information to the experimenter, which picked up the appropriate inducer from a lateral container and placed it on the table either sagittally in front of participants (h1-v1) or on their right side (h2-v2). At this point, the experimenter gave a go signal indicating participants to press the spacebar of the keyboard with their left hand, which caused the shutter glasses to open and then close (250 ms each) for 30 times (~7.5 s in total), such that they could see the test mimicking a visual exploration of the inducer (v1-v2); or they touch the inducer ball on their side for 30 times, such that they could feel it haptically using the thumb and index fingers of the right hand (h1-h2). Once this inducing phase was terminated, the shutter glasses had been closed after the 30th visual presentation of the inducer (v1-v2), or were still closed (h1-h2). Options v1 and v2 were chosen for visual inducing conditions, whereas options h1 and h2 were chosen for haptic inducing conditions. The only exception regarded condition v2 where participants rotated their head to the right ~ 45 degrees to observe the inducing ball (see top right of Figure 3.1).

As soon as the inducing phase ended, the experimenter removed the inducer from its position and placed the test ball in front of participants. A second go signal was then given, indicating to participants that they had to press the spacebar again in preparation for grasping ('test phase'). This

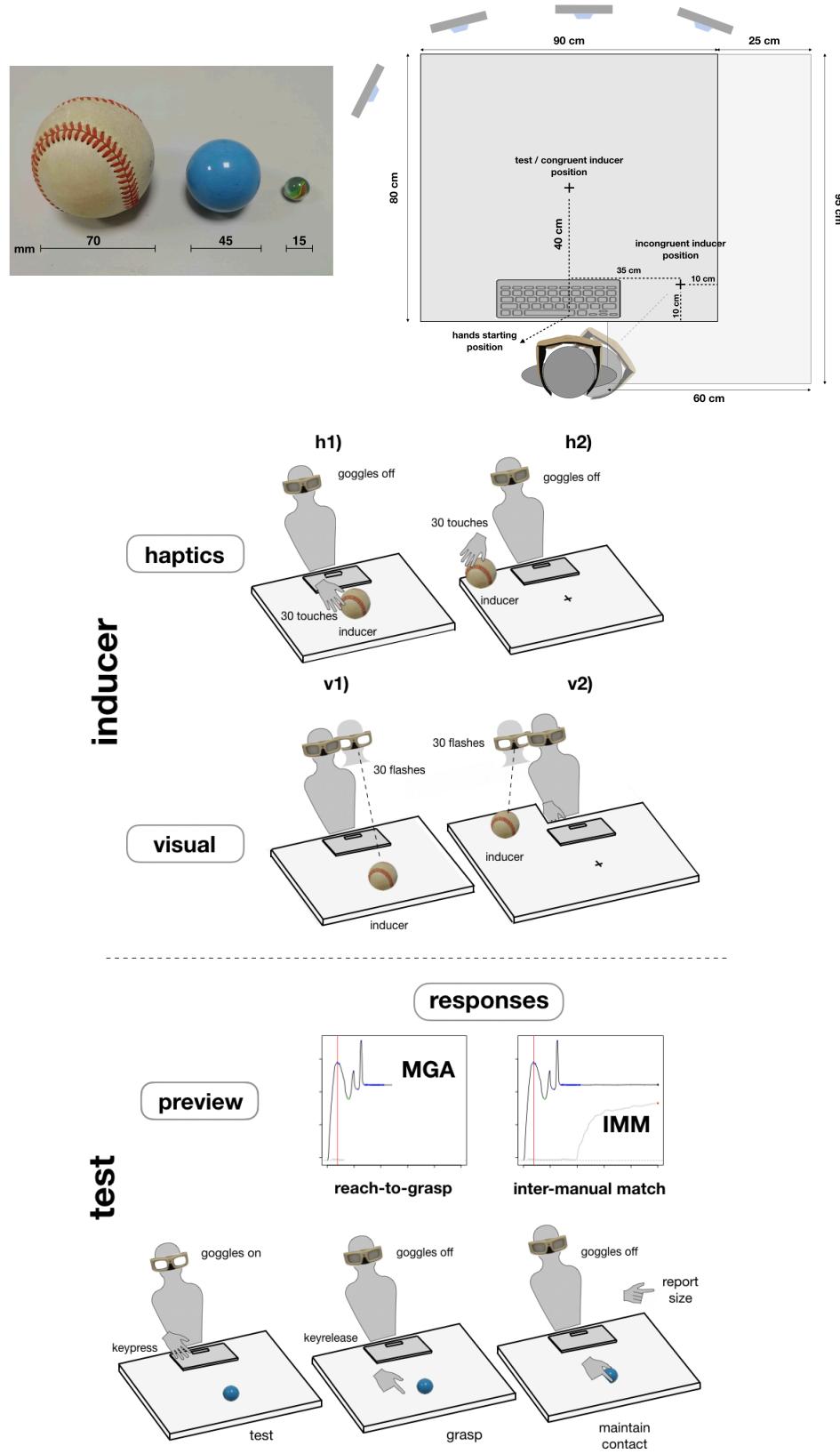


Figure 3.1. Top left: The stimulus set. Top right: The experimental setup viewed from above. The measures of the shaded grey area refer to the panel used to extend the table in the ‘visual incongruent’ condition (v2); The other measures are relative to other three conditions. Middle panel: The inducing phase. The experimenter placed

the inducer ball on the table in front of participants (h1 or v1) or on the right corner of the table (h2 or v2) according to the experimental condition (i.e., the spatial congruency). Then, participants started the inducing phase by visually (v1 or v2) or haptically (h1 or h2) exploring the inducer ball according to the experimental condition (i.e, the sensory inducing). Bottom panel: The test phase. Participants prepared and then executed the grasp for the test after an ad-libitum preview time window; Then, they brought their left hand forward and manually matched the size of the test still holding it in the right hand.

second spacebar press opened the shutter glasses, which remained opened until the participants' hand released the spacebar to initiate the grasp. Thus, participants could observe the test for as long as they wished in preparation of the action. Once they lifted the hand from the spacebar, however, the glasses closed and the action was performed without vision. In addition, the spacebar release caused the experimental program to start recording the kinematics of the responses. After participants had grasped the test, they were requested to continue holding it with the index and thumb of the right hand to report the ball's perceived size by opening the index and thumb of the left hand (Figure 3.1, right panel). The left hand index-thumb aperture was maintained until an acoustic signal informed that the trial (and the kinematics recording) ended. The recording time from the spacebar release to the end trial signal lasted 10 s, giving participants ample time to perform the whole sequence.

Measures and design

We measured two dependent variables: the maximum in-flight grip aperture (MGA) of the right hand index and thumb fingers, during the reach-to-grasp tasks; and the intermanual size match (IMM), that is, the aperture of the same two digits in the left hand at the end of the matching task. The independent variables were the size of the inducing ball (large, medium, or small), the sensory induction (haptic or visual), and the spatial congruency of the inducing-induced pair of balls (congruent or incongruent). Each inducing ball was presented 20 times. Thus, each of the four conditions (see previous section) was assigned to one 60-trial block (totalling 240 trials per participant).

The four blocks were counterbalanced across participants over different days. Each block was further subdivided into 5 sessions of 12 trials to reduce fatigue and manage smaller chunks of data at any given time. Inducer size was randomized within sessions. Overall, each block required about one hour to complete and the whole experiment therefore lasted about 4 hours.

Data validation: MGA and IMM

The kinematics of all trials were screened for atypical grasping profiles. Trials that met the following criteria were included in the analyses: 1) for the right hand, plotting the distance between the thumb and index as a function of time revealed an initial unambiguous peak (the MGA) followed by two successive peaks (the two additional finger contacts with the test ball); 2) for the left hand, the corresponding distance evolved rapidly and then remained approximately constant until the end of the recording period (the IMM). Trials classified as incorrect were discarded before analysis. According to these criteria, data validation resulted in the exclusion of only 13 datapoints (~ 0.5%) based on criterion 1 and 12 datapoints (~ 0.5%) based on criterion 2.

Analyses: MGA and IMM

The MGA of the right hand and the IMM of the left hand were computed from the kinematics records by means of custom-made R scripts based on the following: for the MGA, by inspecting the vector of the index-thumb distances and then choosing, among the three largest distances, the distance that occurred earlier in time (see red vertical line in the MGA plot of Figure 3.1); for the IMM, by noting the last value of the vector of the index-thumb distances (see red dot in the IMM plot of Figure 3.1). The qualitative pattern of the data was first evaluated by plotting the MGA and the IMM as a function of inducer size individually for each participant in each condition (see Figure 3.2). As expected, these plots revealed individual differences in the average value of

both measures (i.e., the intercepts of the linear model fitting the individual datapoints). Given that these differences are irrelevant to the current experimental question, we re-expressed all MGAs and IMMs by subtracting individual averages in the baseline conditions (medium inducer) (i.e., a centering variable procedure, see Enders & Tofghi, 2007; Kreft, Leeuw, & Aiken, 1995). Thus, this yielded a new plot which represented inducer effects as deviations from the baseline average, with negative values signalling a shrinking effect and positive values signalling an enlarging effect (Figure 3.3), which we describe in detail in the next sections below. By visual inspection of this plot, we also deemed appropriate to remove datapoints that were excessively far above or below from zero. Thus, extreme values were identified as higher or lower than a cut-off chosen at ± 15 relative (given a group standard deviation of ~ 5 , this corresponded to values 3 times higher or lower); This resulted in the exclusion of 28 IMM ($\sim 1.2\%$) and 80 MGA ($\sim 3.3\%$) datapoints.

Statistical approach

IMM and MGA relative values were modelled with linear mixed-models (LMMs) using the function *lme* from the *nlme* package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). In contrast to traditional analysis of variance, which uses ordinary least-squares, LMM uses maximum-likelihood estimation calculating the likelihood-ratios (λ_{LR}) between models. This has several advantages. First, it allows to predict participant-by-participant variation in model parameters (random effects) and to discount these individual differences to compute within-participant confidence intervals (CIs) around estimates of fixed effects (i.e., the experimental conditions). Second, LMM frees from drawbacks typically associated with ANOVA models (see Baayen et al., 2008). Third, LMM uses the Akaike information criterion (AIC, see Symonds & Mousalli, 2011) that allows to determine the goodness of fit of models by comparing AICs (ΔAIC). Fourth, LMM allows comparisons across

conditions based on CIs around estimates instead of traditional null-hypothesis tests, in accord with current recommendations on analytical approaches in psychology and behavioural neuroscience (see Cumming, 2014; Kline, 2004).

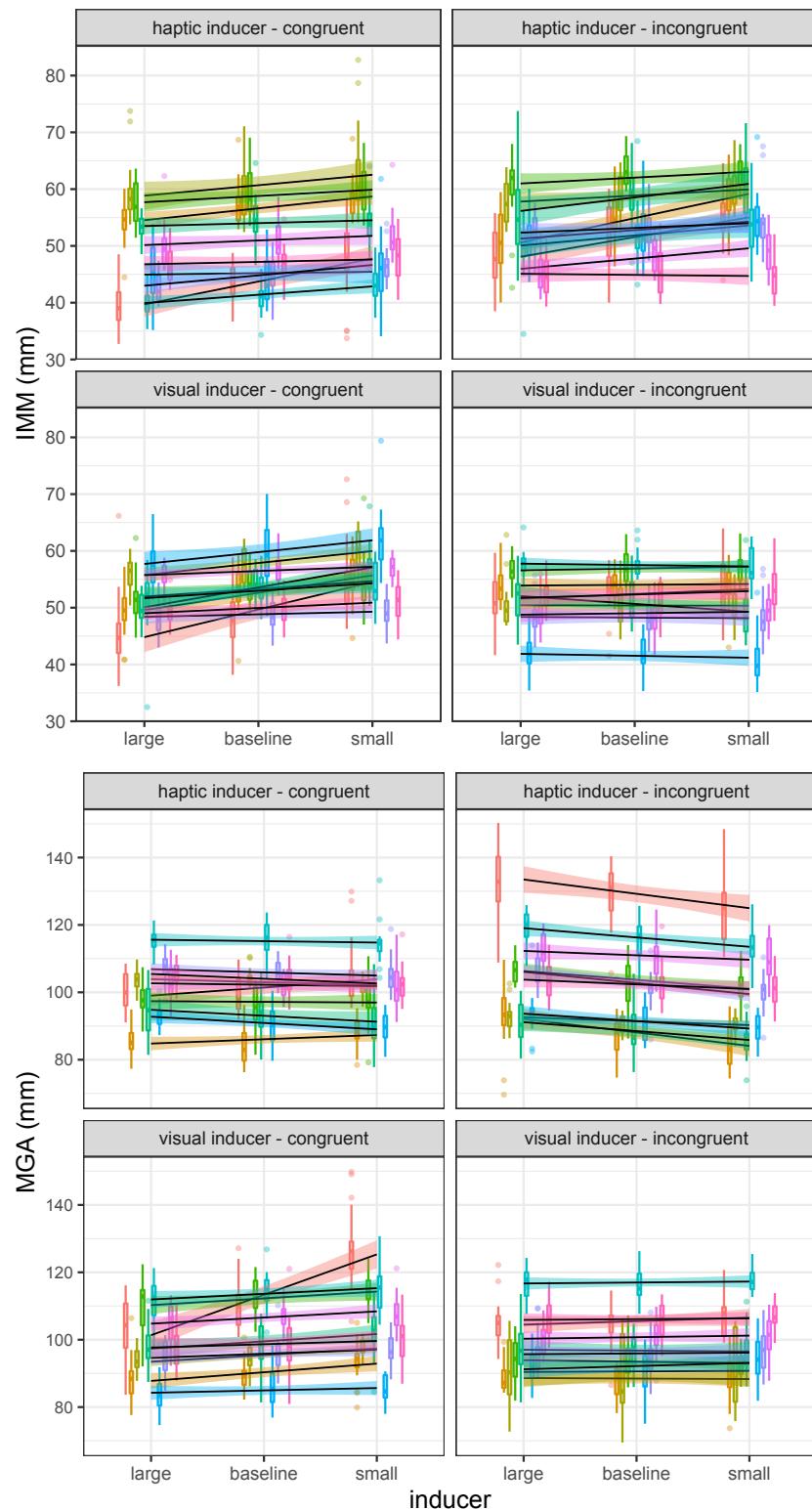


Figure 3.2: IMM (upper plots) and MGA (lower plots) absolute values as a function of the inducer size (x-axis), sensory induction (first and second rows: Haptic; second and third rows: Visual), and spatial congruency (left column: Congruent; right column: Incongruent). Each color identify a different participant. Individual data at each inducer size and in each condition is displayed as boxplot and summarized by a linear model (black line: individual slope; coloured shaded area: 95% CIs). As can be gauged by visual inspection of these plots, individual fits differ in slopes but not in intercepts; Thus, a better view of the data is presented in Figure 3.3 after having expressed datapoints as relative values (see text for details).

Results

Figure 3.3 presents the IMM (upper plots) and MGA (lower plots) data as a function of the inducer size (large, medium, and small), the sensory inducing (first rows: Haptic; second rows; Visual), and the spatial congruency (left column: Congruent; right column: Incongruent). Both variables are re-expressed as deviations from the average of the relevant baseline (see Analyses section above). Colors identify participants, which show similar trends within each of the eight plots. These trends are most clearly summarized by the black lines, which were plotted based on the average of the relevant eight intercepts and slopes from the individual linear fits (coloured lines). Last, grey filled circles are plotted as the mean value obtained by averaging the individual means.

Intermanual match (IMM)

Haptics inducers

The first row of Figure 3.3 presents the IMM data when inducers were presented haptically. In the spatial congruent condition (left plot), finger apertures decreased (or increased) when inducers were larger (or smaller) relative to baseline. This is the familiar Uznadze size-contrast in vision (Bruno, Garofalo, Daneyko & Riggio, 2018), which has been shown to affect not only perceptual reports, but also the MGA in grasping (Uccelli, Pisù, Riggio, &

Bruno, 2019). Here, IMM showed a consistent size contrast pattern in essentially all participants (see coloured slopes). In the spatial incongruent condition (right plot), finger apertures clearly showed again the size contrast effect. Thus, having acquired haptic information about the size of the inducer in a different spatial position is sufficient to affect the perceived size of the test.

Visual inducers

The second row of Figure 3.3 presents the IMM when inducers were presented visually. In the spatial congruent condition (left plot), finger apertures showed size contrast, as expected given the previous results of Uccelli et al. (2019). In contrast, when in the spatial incongruent condition (right plot) finger apertures did not show either a shrinking or an enlarging effect. This is an interesting result suggesting that spatial congruency is crucial for inducing a visual size contrast in a temporal context.

Max grip aperture (MGA)

Haptics inducers

The third row of Figure 3.3 presents the MGA data when inducers were presented haptically. In the spatial congruent condition (left plot), MGAs did not show a clear pattern; Some slopes were positive (i.e., the Uznadze illusion), others were negative (i.e., the inverse of the Uznadze illusion), and others were almost flat. Overall, the average fit indicates the absence of any group effect. Accordingly, the haptic exploration of inducers does transfer in perceptual judgements of the test size, but it is not the same for the representation of size for grasping. In the spatial incongruent condition (right plot), MGAs were smaller (or larger) when inducers were smaller (or larger) relative to baseline, as indicated by the individual and average fits. That is the

opposite of the Uznadze illusion. This is an unexpected, surprising result. Indeed, one would expect a null effect (following the TVSH), as happens in the spatial congruent condition, or at least the Uznadze size contrast effect. What can be drawn from these results is that the haptic exploration of inducers returns different outcomes in perception and action. We discuss the interpretation of this finding in the next section.

Visual inducers

The fourth row of Figure 3.3 presents the MGA data when inducers were presented visually. In the spatial congruent condition (left plot), MGAs revealed the Uznadze illusion. As these experimental conditions are substantially the same as those used by Uccelli et al. (2019), this result confirms that MGAs are affected by a visual size contrast induced in a temporal context. In contrast, in the spatial incongruent condition (right plot) MGAs did not show either a shrinking or an enlarging effect. That is, spatial congruency is crucial to detect the Uznadze illusion for both IMM and MGA responses.

Modelling

Participants were treated as the random factor. The inducer size and the experimental conditions were treated as fixed factors. Thus, the former consisted of a three-level factor, while the latter was treated as a unique four-level factor instead of two separate factors of two levels each. The following procedure was applied to both IMM and MGA relative values. First, we compared the fit of a generalized least squares (GLS) null model with fixed intercept (1) with that of a null model with random intercept (2) using a maximum likelihood criterion. Then, the fixed factor ‘inducer size’ was added as a fixed effect generating model (3) and compared to model (2). Last, the

'experimental condition' factor was added as a fixed effect generating model (4) and compared to model (3).

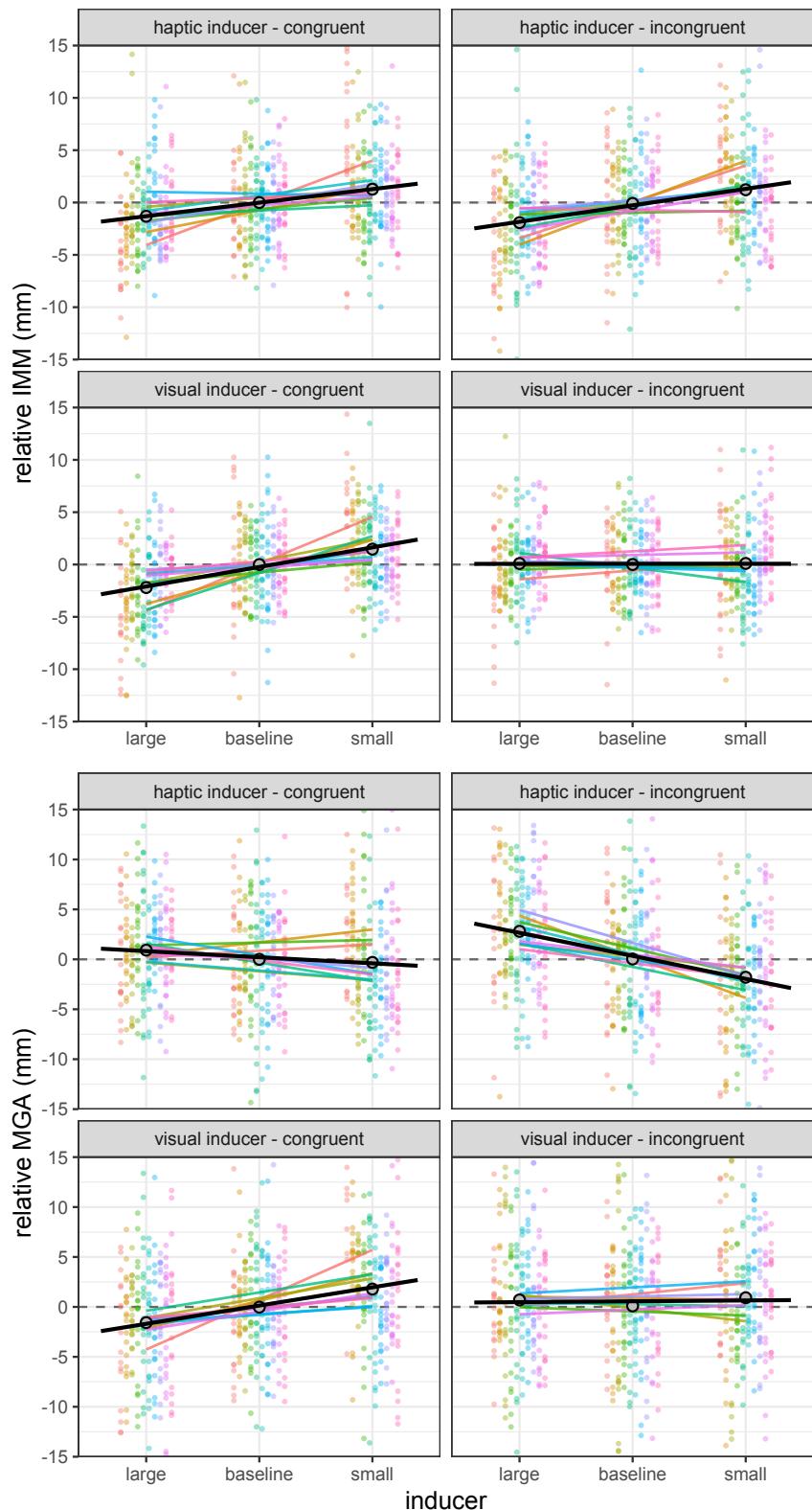


Figure 3.3: IMM (upper plots) and MGA (lower plots) relative values (i.e., by subtracting individual averages of the baseline conditions) as a function of the inducer size (x-axis), sensory channel (first and third rows: Haptics; second and fourth rows: Visual), and spatial congruency (left column: Congruent; right column: Incongruent). Colors identify participants. Points represent individual IMM and MGA in each condition. Positive or negative values on the y-axis indicate a finger aperture higher or lower than zero (i.e., the baseline), respectively. Coloured lines: A linear model fitting the datapoints as a function of the inducer size summarizing the individual data. Black solid line: The average fit in each condition obtained by averaging the individual intercepts and slopes. Grey filled-circles: Average shrinking (below zero) or enlarging (above zero) effect resulted by averaging the individual means at each inducer size. Dashed horizontal grey line: The no-difference value from the baseline if finger apertures were not affected by the inducer size.

For the IMM data, model (2) did not reveal a better fit than model (1) [$\Delta\text{AIC} = 2$; λ_{LR} : $\chi^2(3) = 0.22$, $p = .63$]. Model (3) revealed a better fit than model (2) [$\Delta\text{AIC} = -125$; λ_{LR} : $\chi^2(5) = 129.56$, $p < .0001$]. Model (4) revealed a fit even better than model (3) [$\Delta\text{AIC} = -34.91$; λ_{LR} : $\chi^2(14) = 52.91$, $p < .0001$]. For the MGA data, model (2) did not reveal a better fit than model (1) [$\Delta\text{AIC} = 2$; λ_{LR} : $\chi^2(3) = 0.00$, $p = .99$]. Model (3) revealed a better fit than model (2) [$\Delta\text{AIC} = -2.82$; λ_{LR} : $\chi^2(5) = 6.81$, $p = .03$]. Model (4) revealed a clear better fit than model (3) [$\Delta\text{AIC} = -86.92$; λ_{LR} : $\chi^2(14) = 104.9$, $p < .0001$]. Thus, LMM revealed that both IMM and MGA data were i) affected by the size of inducers and, crucially, ii) modulated by experimental conditions. This confirmed the qualitative patterns observed in Figure 3.3.

Estimate of effects

Given that model (4) has revealed the best fit, we computed from it the estimates of effects and their relative CIs. Figure 3.4 presents these effects with error bars (95% CIs) as a function of inducer size and experimental conditions. Comparisons can be performed directly by evaluating the distance of CIs from the baseline (i.e., zero). For IMMs (upper four plots), CIs of large and small inducers do not overlap (confirming the Uznadze illusion) in all conditions except the visual incongruent condition; for MGAs (lower four

plots), CIs of inducers do not overlap in the visual congruent condition (confirming the Uznadze illusion) and in the haptic incongruent condition (confirming the inverse Uznadze illusion), whereas do overlap in the other two conditions.

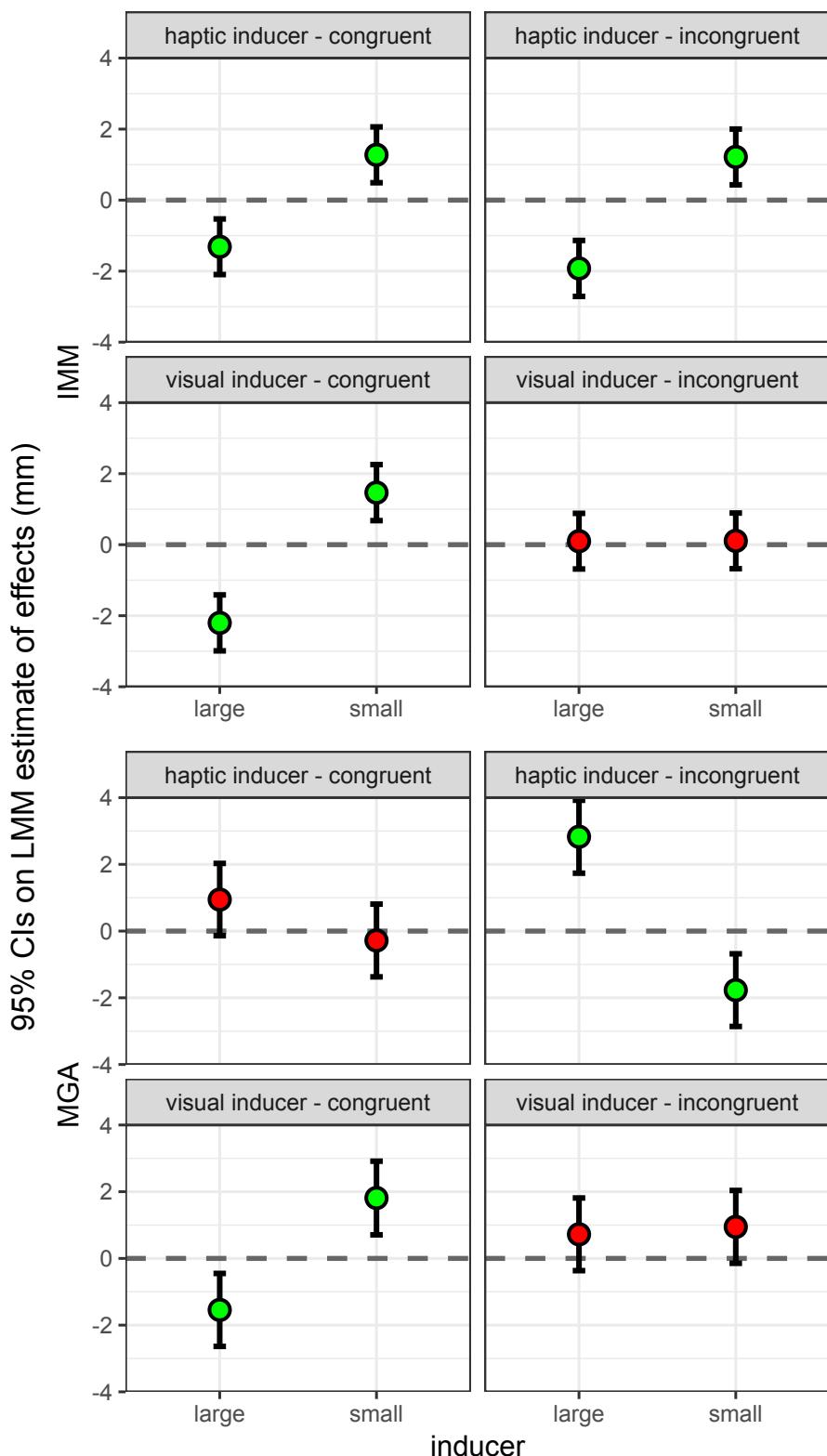


Figure 3.4: Linear mixed model (LMM) estimates of effects of IMM (upper plots) and MGA (lower plots) relative values as a function of the inducer size (x-axis), sensory channel (first and third rows: Haptics; second and fourth rows: Visual), and spatial congruency (left column: Congruent; right column: Incongruent). The dotted horizontal grey line corresponds to the baseline condition (i.e., the intercept parameter of the model). Error bars: CIs (95%) of effects as calculated in the model. Green filled-circles: Significant effects of large and small inducers relative to baseline. Red filled-circles: Non-significant effects of large and small inducers.

Discussion

We interact with objects countless every day. Frequently, we grasp an object after having seen or touched a previous different object. Here, we investigated whether previous visual or haptic information of a first object affects the size representation of a second object. Whether the brain computes different size representations remains a long-standing debate in cognitive neurosciences, in particular whether actions are sensitive to stimulus-contextual information. Results revealed that size representations of perceptual and motor responses did not dissociate with visual inducers, whereas did dissociate with haptic inducers. Surprisingly, we found that motor responses showed either the Uznadze size contrast, the inverse effect, or no effect at all depending on which conditions the inducers were presented in. This represents of a two-pronged dissociation between perception and action which has been never documented before. In the next paragraphs, we discuss results and providing our interpretation condition by condition.

Visual inducers

We start by discussing visual inducers as they have shown the simplest outcome. In the visual congruent condition, both IMM and MGA did show shrinking and enlarging effects. This is unsurprising, as this finding consists of the familiar Uznadze illusion already documented in Uccelli et al.'s work (2019) where both perceptual and motor responses showed size contrast

effects. In contrast, in the visual incongruent condition both IMM and MGA did not show size contrast. Thus, spatial congruency is essential to generate size contrast effects between two objects. A reasonable interpretation is that local relational signals of sizes receive less importance based on perceptual grouping rules informing that the two objects do not belong with each other. Accordingly, no size contrast effect should arise if inducing stimuli are presented in a different position relative to the test. This interpretation, moreover, is consistent for both IMM and MGA data as both responses did not show dissociation with both congruent and incongruent conditions. This first finding, therefore, does not support distinct size representations between perception and action as stated by the TVSH.

Haptic inducers

We now discuss the results of haptic inducers. In the haptic congruent condition, IMM and MGA revealed a dissociation. Previous haptic information of large (or small) inducers did shrunken (or enlarged) the IMM, but not the MGA, i.e. the two measured dissociated. However, a more careful inspection of MGA data suggests that some participants did show a positive slope, others a negative slope, and others an almost flat slope (see coloured lines in the ‘haptic inducer - congruent’ plot of Figure 3.3). This suggests the presence of two contrast processes. One is associated with the contrast between the sizes of inducers and tests. That is, the (blinded) haptic exploration with fingertips of large (or small) inducers might generate a size contrast that makes the test appear smaller (or larger). Accordingly, this multisensory process explains the Uznadze effect on both the IMM and MGA. However, a second process affects the internal schema of the hand. That is, the same haptic exploration with fingertips of large (or small) inducers might generate a size contrast that makes participants feel their hand as smaller (or larger). Thus, the internal hand schema of participants is shrunken (or enlarged) before preparing the grasp. If the hand is shrunken, finger aperture will

increase to ensure a safe grip; In contrast, if the hand is enlarged finger aperture will decrease to ensure a more accurate grip, thus in turn MGAs are larger (or smaller) after having touched large (or smaller) inducers (i.e., the exact opposite pattern of the Uznadze illusion). Accordingly, this modification of the hand schema explains why participants showed negative slopes. Moreover, we speculate that these two processes enter into conflict with each other. Indeed, if a process promotes the Uznadze size contrast and the other process promotes the inverse effect, the outcome should be an (approximately) null effect. Actually, this could be true for some participants that showed a nearly flat slope (see again the ‘haptic inducer - congruent’ plot of Figure 3.3). Whether the two processes tend to nullify or one of them prevails over the other one is an intriguing question that can be explored in future research. At present, what is interesting here is that perceptual and motor responses dissociated.

Lastly, we discuss the haptic incongruent condition. Here, perceptual and motor responses dissociated once again: the IMM revealed the Uznadze illusion whereas the MGA revealed the exactly inverse direction. In contrast to the spatial congruent condition, here no multisensory integration between inducers’ sizes and the hand schema could have occurred, as the haptic exploration of inducers did not spatially coincide with the test. Therefore, no size contrast was supposed to take place between inducers, leaving solely the modification of the internal schema of the hand. Accordingly, large inducers shrunken (or enlarged) the hand returning larger (or smaller) MGAs. Such ‘size assimilation’ is a robust effect evident in all participants (see the coloured negative slopes in the ‘haptic inducer - incongruent’ plot of Figure 3.3). This pattern resembles the results found by Bruno and Bertamini (2010), where the exposure to a large (or small) fake hand led participants to overestimate (or underestimate) the perceived size of the test. We claim therefore that the present results fit well with an interpretation based on the hand schema modification. We propose that the brain rapidly recalibrate haptic signals using

an internal model of the hand, and this modification is carry over during the preparation of an upcoming visuomotor process such as grasping.

Conclusion

In the cognitive neurosciences, it is generally accepted that vision-for-action and vision-for-perception represent object sizes in different manners. In general, this claim is based on results showing that motor responses are immune to stimulus-contextual effects in contrast to perceptual judgements. This conclusion generated the belief that actions such as grasping rely on absolute rather than relative information, in both space and time. In the present work, we found that the Uznadze illusion revealed a two-pronged dissociation between perception and action. With visual inducing, perceptual and motor responses did not dissociate either if the two objects shared or not the same spatial position. In contrast, responses did dissociate with haptic inducing. Whereas perceptual judgements showed the Uznadze illusion, motor responses revealed a size assimilation effect or a null effect depending on whether the two objects shared or not the same spatial position. This work demonstrates that the size representation for grasping is sensitive to previous sensory information and, for the first time, that the representation differs depending on factors that seem related to multisensory integration and the internal hand schema rather distinct representations between perception and action. We suggest that such factors should be taken into account in designing future research on behavioural action-perception dissociations to avoid falling into simplistic dichotomous explanations.

Chapter 4

Action preparation in grasping reveals generalization of precision between implicit and explicit motor processes

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Abstract

It is often claimed that merely seeing a graspable object can elicit the implicit representation of a potential grasp. But can this representation affect the explicit execution of an actual grasp, and if so, how? In an open-loop paradigm, we instructed participants to grasp small, medium, or large test disks with the appropriate grip configuration (pincer, tripod, or pentapod). Before the presentation of these tests, we presented congruent or incongruent distractors. To assess interactions between implicit (putatively elicited by the distractors) and explicit (actually executed) sensorimotor processes, we measured preview reaction times (as an index of action preparation) and grasp kinematics (as an indicator of sensorimotor representations for motor control). Results indicate that action preparation is indeed affected by the presentation of preceding distractors. However, costs in action preparation were measured only when the first, implicit process was less precise than that of the actual grasp. We suggest that an interaction occurs at the level of sensorimotor processes through a mechanism which generalizes a precision parameter. We interpret these findings in relation to processes involved in real-time motor control and within the framework of theories of motor cognition.

Introduction

It is well known that the human higher-level visual system exhibits two main cortical processing streams. The so-called ventral stream projects from V1 (the primary visual cortical area) to IT (the inferotemporal cortex). The so-called dorsal stream, conversely, projects from V1 to PPC (the posterior parietal cortex). What are these streams for? That is, do these distinct neural structures subserve different functions? Ungerleider and Mishkin (1982) proposed that the ventral stream processes object identity whereas the dorsal stream processes space. Underpinning this “what” vs. “where” distinction were earlier observations on the behavioral consequences of brain lesions in humans (Holmes, 1918; Newcombe, 1969; for reviews see Cooper, 2012; Cooper and O’Sullivan, 2016) and on cortical vs. non-cortical visual pathways in non-human animals (Schneider, 1969). Goodale and Milner (1992; Milner & Goodale, 1995, 2006; 2008) refined this proposal, suggesting that the difference may lie not in what visual information is processed, but on the purpose of this processing. In the ventral stream, visual processing aims at achieving representations that remain invariant under changes in the conditions of observation, enabling object recognition and identification (“vision-for-perception”). In the dorsal stream, conversely, processing aims at monitoring parameters relevant to limb movement, enabling the online control of goal-directed movements (“vision-for-action”). Milner and Goodale’s proposed division of labor is generally referred to as the “two-visual-systems hypothesis” (TVSH).

The TVSH has provided a framework for interpreting data from diverse approaches such as neuropsychological patient studies (e.g. Goodale et al., 1991), brain imaging studies (e.g. Faillenot et al., 1997), and combination psychophysics-kinematics studies (e.g., Aglioti et al., 1995). In addition, the TVSH has proved heuristic in stimulating research on the functional interpretation of the dorsal-ventral distinction. One important issue here has been the degree of encapsulation within vision-for-action. Is this subsystem

completely independent, or does it interact with other visual processes and if so, when and how? Although the original version of the TVSH stressed independence, later revisions of the model have explicitly recognized the need to study how vision-for-action may interact with other visual processes (e.g. Goodale, 2011; Milner, 2017; Whitwell et al., 2014). Here we focus on one potential form of such interactions, namely, whether seeing contextual objects before acting on a different test object affects how the action is prepared and executed. The theoretical motivation of such question is developed in the paragraphs that follow. According to the TVSH, visual information is coded in relation to different spatial frameworks depending on the processing goal: object recognition or online motor control. These two processing goals are subject to different computational constraints. Object recognition requires to represent features such as size, shape, and orientation in relation to the location of other objects. Such object-relative representations promote constancy under changes in viewing conditions, a key requirement for recognition (Biederman, 1987; Marr, 1982; Milner & Goodale, 2006). Online motor control, conversely, requires that features be coded with respect to effectors. Effector-relative spatial representations provide the motor system with the online information required to configure limb trajectories and hand shaping for the intended actions. As a consequence of these differing constraints, vision-for-perception emphasizes relatively long-lasting spatial and temporal allocentric relations. Vision-for-action, conversely, focuses on the here-and-now, fast-decaying relations between objects and effectors to produce continuously updated egocentric representations. Thus, in the TVSH vision-for-action is mainly conceived as a system for real-time control (Westwood and Goodale, 2003) and should be unaffected by the temporal context preceding a movement. In a comprehensive recent review, Schenk and Hesse (2018) examined the empirical support for such a strong prediction, which they called the “dorsal amnesia” hypothesis, and concluded that dorsal amnesia is not generally supported. We take this as a call for further research on the nature of potential temporal interactions (or lack

thereof) within specific motor tasks that may relate to specialized cortical networks (see Schenk et al., 2011). This line of research promises to further qualify functional subdivisions within the primate visual systems beyond useful first-order approximations suggested by dichotomous models such as the TVSH.

Our starting point is the hypothesis that seeing an object elicits object-related motor representations even if no action is executed and even if no other processing of the object is required by the task (see for instance Chao and Martin, 2000; Ellis & Tucker, 2000; Grafton et al., 1997; Grezes & Decety, 2002; Tucker & Ellis, 1998, 2001; 2004). We call this the automatic visuomotor coding hypothesis. Based on this hypothesis, one might expect that seeing an object having size and shape that make it graspable relative to a typical human hand should automatically evoke a motor process for grasping. The so-called “canonical” neurons observed in monkey area F5 are generally believed to constitute a candidate neural mechanism underpinning the automatic elicitation of motor representations from visual information (Rizzolatti & Gentilucci, 1988; Murata et al., 1997). In humans, evidence from visuomotor priming studies (Craighero et al., 1996; Craighero et al., 1998) also supports the idea that seen visual features elicit motor representations. However, it is currently not clear whether motor representations elicited from seeing objects will affect the actual planning or actual execution of a later object-directed action, and how this might take place (but see, Hesse et al., 2008; Seegelke et al., 2016). A more detailed account of visuomotor priming studies is provided in the following sections along with corresponding predictions with regard to our study.

Here we capitalized on a recent study by our laboratory (Uccelli et al., 2019) which exploited a visual version of the Uznadze size-contrast illusion. In the Uznadze illusion, the same object is perceived as smaller when preceded by a larger object and as larger when preceded by a smaller object (Uznadze, 1966; Bruno et al., 2018). To test whether vision-for-action remains unaffected

by this form of size contrast, as predicted by the TVSH, Uccelli and collaborators compared the maximum in-flight finger aperture (maximum grip aperture, MGA) for grasping and the indicated finger aperture in cross-modal size matches as a function of the size (smaller or larger) of a preceding distractor. In contrast with the TVSH prediction, they found that participants opened their fingers more when grasping targets preceded by smaller inducers, and less when grasping targets preceded by larger inducers (in comparison with a baseline condition with inducers having the same size as the test). This result runs counter the predictions of the TVSH. However, it does not specifically address automatic visuomotor coding. In this paper, we modified our earlier paradigm to perform such a test.

To test whether motor processes associated with grasping an object are modulated by motor processes elicited by previously viewing another object, we varied the size of distractor and test stimuli and explicitly associated different types of precision grips (Napier, 1956) to each level of size. Specifically, small stimuli were associated with pincer grips (two fingers), medium stimuli with tripod grips (three fingers), and large stimuli with pentapod grips (all five fingers). In an open-loop paradigm, we asked participants to grasp test objects using the associated grip types. Presentation of test objects was preceded by that of distractors that putatively elicited congruent or incongruent grips. Our specific objective was therefore to explore potential interactions between a hypothesized first, implicit motor representation and a second, explicit motor process. Critically, we focused on the planning phase of the movement, i.e., the sensorimotor computations which are carried out before movement initiation. To evaluate the preparatory phase of the action, we assessed the brief temporal interval spent by the participant observing the target before grasp initiation (preview reaction times, PRT). As preview reaction times were completely under the control of participants, we expected that their duration may reveal benefits (shorter PRTs) or costs (longer PRTs) as a consequence of interactions with implicit motor representations elicited by the distractors. That is, as the action goal

and stimulus position were kept the same, we attributed differences in PRTs to interactions between implicit and explicit motor processes in the planning phase of the movement. Different patterns of benefits and costs are predicted by different hypotheses about the nature of such interactions, as detailed in the next paragraph. To evaluate the actual execution of the grips, we recorded grip kinematics and measured the MGA. Predictions for the pattern of this kinematic marker are developed in the paragraph following the next.

Predictions

Preview reaction times predictions

Real-time motor programming

According to the real-time view of motor control, actions are guided on the basis of fast-decaying, continuously updated egocentric representations (Westwood and Goodale, 2003). This view predicts that each new grip will be programmed anew without taking into account visual information that may have been available before the presentation of the grip target. Thus, preview reaction times should be unaffected by the congruence of the target with a previously presented distractor. Under this hypothesis, therefore, we should expect that times might vary as a function of the size of the target (and its associated grip), but remain constant for each target size at all levels of distractor size.

Visuomotor priming

In visuomotor priming, a prime stimulus yields benefits or costs in reaction times for a motor response that can be congruent or incongruent with a feature of the prime. For instance, Craighero et al. (1996, 1998) asked participants to grasp an oriented bar after the on-screen presentation of the same bar having the same or different orientation (or of a no-prime baseline), and measured reaction times for initiating the response. Craighero and collaborators reported shorter times in the congruent condition and linked

them to the sustained influence of prior visual information. The findings of Craighero and collaborators have been replicated and extended in numerous other studies (Hesse et al., 2008; Roche & Chainay, 2013; Seegelke et al., 2016; Valyear et al., 2011). However, for various reasons such as the nature of the prime (which is often a picture on a computer screen rather than an actual object), the nature of the response (which may be regarded as different from an actual, object-directed, performative action), the visibility of the hand during the motor response (which is typically prevented in these studies), and the temporal regimes (which correspond best to those of memory guided actions), it has been argued that this task engages semantic representations coded by the ventral system rather than truly sensorimotor processes (Cant et al., 2005; Garofeanu et al., 2004; but see, Hesse et al., 2008; Seegelke et al., 2016). While the debate on the interpretation of visuomotor priming continues, this literature indicates that a plausible expected pattern of results in our paradigm may be that congruent distractor-test pairs facilitate movement preparation (as indexed by shorter times), whereas incongruent distractors slow movement preparation. Importantly, this hypothesis predicts that costs and benefits should depend solely on the congruency between the distractor and target stimulus. Therefore, we should expect to observe benefits with all congruent distractor-test pairs, independent of the associated grip type, and costs for all incongruent ones.

Finger-based visuomotor priming

Given the specifics of our task, another form of visuomotor priming is conceivable. Consider motor programs for pincer, tripod, and pentapod precision grips. An obvious difference between them is that they require kinematic parameters only for the index and thumb, or for only index, thumb, and middle finger, or for all five fingers. Now consider two types of trial in our task. Suppose first that a large distractor is followed by a small target. If the large distractor (which is associated with a pentapod grip in our task) pre-activates a motor representation including kinematic parameters for all five

fingers, this preactivated representation may be effective in facilitating a small test (which is associated with pincer grip), as the fingers in this response (index and thumb) could in principle inherit kinematic parameters from the preactivated five-finger representation. Now suppose that the opposite takes place: a small distractor (pincer grip) is followed by a large test. In this case, only two fingers are pre-activated and the other three might therefore need further processing. Thus, one might expect a cost on motor programming (again, as indexed by times). Although we are not aware of behavioral evidence of such phenomenon, neuroimaging results indicate that number of digits may recruit different portions of premotor, motor, and somatosensory areas (Cavina-Pratesi et al., 2018). In general, finger-based priming predicts that benefits and costs will depend on the number of fingers required to respond to distractor and test, respectively. Whenever they are the same, no effect is expected. Whenever distractor fingers are less than test fingers, a cost is expected. Whenever distractor fingers are more than test fingers, a benefit is expected.

Generalization of precision

Finally, it is possible to hypothesize that costs and benefits in movement preparation will depend on the level of precision required in pre-programming hand shaping as a function of stimulus size. Although in our task all motor responses can be classified as “precision” grasps (as opposed to coarser “power” grasps involving the hand palm), actual degrees of required sensorimotor precision are likely to depend on stimulus size (i.e., width). In psychophysics, it is well known that differential thresholds are directly proportional to stimulus magnitude (i.e., Weber’s law, Fechner and Adler, 1966/1860). In motor control, it is also largely accepted that movement time is inversely proportional to target width (i.e., Fitts’ law; Fitts, 1954). Although it is not obvious how they would apply to our task (but see Arbib et al., 1985; Hoff & Arbib, 1993; Wing & Fraser, 1983), both principles can be interpreted as reflecting enhanced precision with smaller targets, due to the need of,

respectively, finer sensory discrimination during perceptual processing or longer online control during movement execution. Similar considerations have been developed also in the context of reach-to-grasp movements (Gentilucci et al., 2003; Bootsma et al., 1994) although there is still debate as to whether Weber's law applies to sensorimotor representations for grasping (see Bruno et al., 2016; Ganel et al., 2008; Smeets & Brenner, 2008; Utz et al., 2015). To see how differences in required motor precision may produce a pattern of costs and benefits in our task, consider again a trial whereby a large distractor is followed by a small target. Assuming that the distractor will automatically elicit a motor representation, this should require a relatively low level of precision due to the larger size. When the participant is then required to grasp a smaller target, a relatively higher level of precision will be required and this might produce a cost on the process of movement preparation. For instance, the motor program may need upgrading to a higher degree of precision, or it may need to be erased and recomputed. Consider now the opposite case, when a small target is followed by a large one. Assuming again automatic elicitation of a motor representation by the initial distractor, this would require a relatively higher degree of precision due to the smaller size. In this case, motion preparation for grasping the test will not need upgrading, as the test will require a lower degree of precision in comparison to the distractor. According to this hypothesis, therefore, asymmetric costs and benefits should be observed depending on whether the precision required by the distractor is higher or lower than that of the test. When precision is higher for the distractor in comparison to the test, it may generalize to motion preparation for the test, resulting in no cost, or possibly even a benefit. When it is lower, motion preparation for the test will need upgrading the precision parameter, resulting in a predicted cost. As we shall soon see, our results from two experiments support this latter hypothesis.

Maximum grip aperture predictions

In our paradigm, a size-contrast effect should be expected at the perceptual level. That is, given the temporal relationship between distractor and target stimuli, target stimuli should be perceived as larger when preceded by the small distractor and as smaller when preceded by the large distractor (Bruno et al., 2018; Uccelli et al., 2019; Uznadze, 1966). Assuming that the MGA can be regarded as an index of the sensorimotor representation of size for the to-be-grasped object (but see, Hesse et al., 2016), predictions can be made concerning whether MGAs will also be affected by the illusory effect. In the current study, this assumption requires a corollary due to the specific nature of the task, which involved two-finger grips as well as grips with more than two fingers. Given that the MGA is estimated from the distance between the index and the thumb, this measure provides a full picture of in-flight hand shaping in the former, but it fails to capture the shaping of the additional fingers in the latter. This may not be a serious limitation, as there is evidence that the third, fourth, and fifth finger tend to move in coordination with the index in multi-digit grasping (Gentilucci et al., 2003; Gilster et al., 2012, Santello & Soechting, 1997). Nonetheless, interpretations of the current study need additional caution as the MGA may not fully assess potential distractor effects on grasping when our test objects called for tripod or pentapod grips. This potential limitation notwithstanding, a consideration of theoretical predictions remains useful, and a test of the results may provide information on the validity of the corollary assumption that the MGA taps into the motor representation of size even in precision grips involving more than two fingers.

Real-time motor programming

According to the TVSH, vision-for-action codes space in continuously updated effector-related frames of reference. Thus, unlike conscious perception, dorsal representations for guiding actions should be unaffected by the spatial and temporal relations between objects which are the basis of perceptual illusions (Milner & Goodale, 2006; Westwood & Goodale, 2003). Under this hypothesis, we would therefore expect grip apertures to vary only as a

function of target size, regardless of the distractor size, that is, of any possible illusory effect affecting visual perception.

Temporal context affects the MGA

Conversely, if vision-for-perception is affected by the temporal context, maximum grip apertures for grasping the target and the perceptual illusory effect should yield similar patterns. Thus, one would expect the intermediate, tripod grips associated to the intermediate-size target to be influenced by the presentation of the distractor stimulus. Said otherwise, participants should open their fingers more after the presentation of the small stimulus, and less after the presentation of the large stimulus, in comparison to the corresponding congruent condition (same distractor and target). This is the pattern observed in our previous paper (Uccelli et al., 2019). Given the similarities between the paradigm implemented by Uccelli and colleagues and the current work, we predict to replicate this finding in the conditions involving intermediate size targets. Predictions for the large and small targets, conversely, are less clear. Under the hypothesis that these should also be influenced by temporal context, one might expect that small targets would yield even smaller MGAs when preceded by larger targets, and that large targets would yield even larger MGAs when preceded by smaller targets. Given the target sizes we chose to use in the current study, however, whether these effects will be detectable is doubtful. First and foremost, our small and large targets were indeed very small and very large. In fact, they were close to biomechanical limits for inter-digit closure and aperture. This implies that MGAs for small and large targets have less chances to vary in the expected directions, which in turn may generate floor and ceiling effects and conceal potential contrast effects. Second, half of the incongruent trials involving small and large targets will be preceded by intermediate size distractors, which imply a weaker size contrast signal than the large and small ones. The combination of these two factors is therefore likely to obscure the effect of distractors due to random variability superimposed on a weak signal. Note

however that such concerns do not apply to tripod grips. For these reasons, we suggest that a strong prediction (stemming from our previous findings, Uccelli et al., 2019) can be made for the MGAs associated to the tripod grasp targets, whereas tests of MGAs associated to other two targets be treated as exploratory.

General methods

We performed two experiments. Here we present their common methodological features. Details specific to each experiment are presented in subsequent sections along with the corresponding results and discussion.

Task

We asked participants to grasp a small, medium, or large disk after a discretionary observation window. The grasp was fully open-loop in that vision of the target was removed at the exact time of initiation of the action. Each of the three disks was paired with a different type of grasp, i.e. the most appropriate grasp for an object having that size. Grasp appropriateness was defined based on the taxonomy proposed by Feix et al. (2015). All were “precision” grasps involving pad opposition but no palmar opposition, but requiring two, three, or five fingers. Based on this classification, we instructed and trained participants to grasp the small disk using a pincer grip (index and thumb pad opposition), the medium disk using a tripod grasp (index, middle, and thumb), and the large disk using a pentapod grasp (all five fingers).

Stimuli

Both experiments involved presenting target stimuli, that had to be grasped, and irrelevant distractors that were simply presented before the targets. For both, we used custom-made wooden disks of 3 different diameters and having the same shape (circles) and color (white, approximately corresponding to a

Munsell value of 8.5). The diameters were 10 mm (small), 35 mm (medium), and 120 mm (large). All disks were 10 mm thick. All stimuli were presented in the center point of a black cardboard panel (approx. 30 x 21 cm) that served both as background and as support for the stimuli.

Apparatus

Participants sat on an adjustable chair in front of a rectangular table (90 x 80 cm). A wireless keyboard was positioned on the anterior part of this table, with the spacebar center aligned with the center of the stimulus, and both in turn approximately aligned with the participant midline. The stimulus was mounted on the center of the stimulus support panel, which was fit to a plastic holder in a quasi-vertical position (Fig. 4.1). The distance between the spacebar and the stimulus support panel was 43 cm. Stimuli were held in the appropriate position on the support panel by means of small magnets plus, for the heavier medium and large disks, two thin metal pins that protruded slightly from the support panel to support the bottom part of the disk circumference. PLATO shutter glasses (Translucent Technologies, Toronto, Ontario, Canada; Milgram, 1987) allowed us to control stimulus visibility (translucent-to-opaque latency: 3-4 ms) during trials, and we used a BTS-DX100 Smart System equipped with four cameras (sampling rate 100 Hz, spatial precision at least < 0.2 mm) to track three passive (retro-reflecting) markers during each grasp. Markers were positioned on the right hand of the participants on the thumb and index nails and on the radial side of the wrist. We used MATLAB R2011b on a Windows 7 personal computer to control trial order and to trigger the shutter glasses as well as the motion capture system.

Measures

Dependent measures were computed from each tracked trial using a custom program developed in the R statistics software (R Core Team, 2017). Preview reaction times (PRT), defined as the duration of the interval defined by the first opening of the shutter glasses (allowing participants to see the targets)

and grasp initiation (which always coincided with the closing of the shutter glasses), were the main dependent variable. In addition, for each trial we measured the maximum in-flight index-thumb aperture (MGA). Finger apertures were measured by calculating the Euclidean distance between the index and thumb markers as a function of time. The MGA for each trial was then computed by identifying the peak value in grip aperture occurring before the fingers contacted the object.

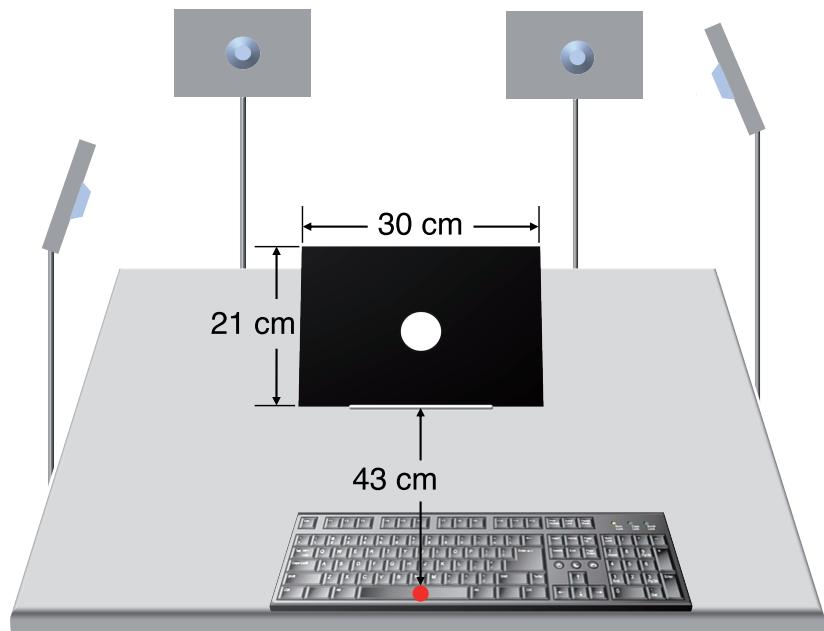


Fig. 4.1. Schematics of the experimental setup for both studies. Participants wore computer-controlled shutter glasses (not shown) which allowed us to control the visibility of the stimuli during trials.

Procedure

Experimental sessions were run by a supervising experimenter who monitored the stimulus sequence while sitting in front of a computer screen, plus an executing experimenter who stood by the experimental table and took

care of stimulus presentation. Before each experimental session one of them gave a brief verbal explanation of the task to the participant. This was followed by ten practice trials that were not recorded. Trial structure was as follows. First of all, the shutter glasses were closed (no vision) to allow the experimenters to mount the appropriate distractor for the trial on the support. Once this was done, one of the experimenters issued a verbal "go" signaling the participant to press and release the spacebar. This caused the shutter glasses to open and close sequentially for five times (opening duration = 250 ms), producing a presentation of the initial distractor that lasted a total of 1250 ms in five intermittent flashes. During this presentation, participants were not requested to do anything but to maintain fixation around the center of the display. Once the presentation of the distractor stimulus was completed, the shutter goggles remained closed. After 2 s, a computer-generated beep was sounded for 1 s. The 2 s period allowed the experimenters to remove the distractor disk and to mount the target disk; the beep served as a second "go", signaling the participant to press again the spacebar. This second press caused the shutter glasses to open again. Thus, the shutter glasses remained close for 2 s, plus the participant's reaction time to the "go" signal. Participants were instructed to keep the spacebar pressed for as long as they needed to prepare a quick and natural grasp, and then to lift the hand and actually perform the grasp. Exactly at the release of the spacebar, the glasses were again closed and a 3 s kinematics recording window started. Participants always reached for and grasped the target, removed it from the panel, put it on the table, and returned to the start position. At the end of the 3 s recording window, the trial ended and the computer supplied the stimulus identifiers for the subsequent trial. The experiment was divided in two sessions separated by a pause of about 10 min to minimize fatigue. Occasionally, due to the mechanics of stimulus identification, selection, and placement, an error occurred. In these cases, the trial number was noted by the supervising experimenter. All trials identified as errors were then repeated in random order at the end of the experiment.

Analysis

Data analyses were performed using R 3.4.0 (R Core Team, 2017). Preview reaction times were analyzed by first removing datapoints that were symptomatic of technical errors or anticipatory responses, or that could be identified as outliers and were then checked for normality. A similar procedure was used for the validation and analysis of maximum grip apertures. Because PRTs showed marked deviations from normality, as is typical of skewed RT distributions, we used the `boxCox` function available in the `car` package in R (Weisberg & Fox, 2011) to identify the most appropriate transformation (see Box & Cox, 1964). In the case of the present studies this turned out to be simply a logarithmic transformation. Accordingly, all statistical testing was performed on the transformed data, but all presented averages and confidence interval limits were transformed back to ms by computing the inverse of the transformation (in this case, this means that our reported measures of central tendency are geometric means of PRTs). Data were modelled using generalized mixed-effect regression using the `nlme` package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). In comparison to traditional analysis of variance, which uses ordinary least-squares, mixed-effects modelling uses maximum-likelihood estimation. This has several important advantages. First, it allowed us to predict participant-by-participant variation in model parameters (random effects) and to discount these individual differences to compute within-participant confidence intervals around estimates of fixed effects. Second, it freed us from drawbacks typically associated with traditional ANOVA models, such as deficiencies in statistical power, individual differences in repeated measures designs, and unprincipled ways of dealing with heteroskedasticity and non-spherical error variance (see Baayen et al., 2008). Third, mixed-effects modelling allowed us to choose between models using the Akaike information criterion (AIC), which offers a principled balance between goodness-of-fit and model parsimony (see Symonds & Moussalli, 2011). Fourth, but not less important, mixed-effects modelling allowed us to perform comparisons across conditions using

confidence intervals around parameter estimates instead of null-hypotheses tests, in accord with current recommendations on analytical approaches in psychology and behavioral neuroscience (see Cumming, 2014; Kline, 2004). Comparisons can therefore be performed directly by evaluating whether confidence intervals cover estimates for baseline predictions in each condition.

Ethical approval

The study was performed in accordance with the ethical standards of the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki), with the ethical standards of the Italian Board of Psychologists (see http://www.psy.it/codice_deontologico.html), as well as the Ethical Code for Psychological Research of Italian Psychological Society (see <http://www.aipass.org/node/26>). Informed consent was obtained from all participants prior to participation.

Experiment 1

Methods

Participants

We recruited 16 participants (8 females and 8 males; age range 23–32) from the University of Parma community. All were right-handed, had normal or corrected-to-normal eyesight, no history of neurological diseases, and were unaware of the purpose of the study.

Design

The design of the experiment resulted from crossing distractor and target stimuli as within-participant independent variables. We used three disk sizes (small, medium, and large) for both the distractor and the target stimuli. This

yielded a total of 9 conditions, of which 3 were congruent (same size and same associated grasp for distractor and target stimuli) and 6 incongruent (different size, different grasp). Congruent conditions were treated as baseline conditions. Each condition was presented 20 times, in randomized order, totaling 180 trials.

Results

Preview reaction times

Preview reaction time data analysis and validation

Preview reaction time data for 10 trials were missing due to technical errors. These trials were preliminary discarded from the overall sample. We then tested for the presence of anomalous values in the distribution. A cut-off value of 150 ms was established to identify anticipatory responses. Based on this criterion, a total of 9 trials were removed. We then used the following criterion to identify extreme values as outliers:

$$\text{abs}(\text{PRT}-\text{median}(\text{PRT})) \geq 3 * \text{IQR}(\text{PRT})$$

That is, we preliminary estimated the median and interquartile range (IQR) of preview reaction times per target for each participant and then calculated the difference between the value and the median for each trial. Values with an absolute difference from the median greater than or equal to 3 times the IQR were identified as outliers. A total of 26 trials met this criterion. Overall, 35 trials (1.22% of the total of valid trials) were discarded. We then proceeded by checking the overall distribution. This was asymmetrical (skewness = 1.28) and leptokurtic (kurtosis = 4.94) as shown in Fig. 2 (top row). To remedy this, we applied a Box-Cox transformation procedure (Box and Cox, 1964) to the raw data. This revealed that an excellent approximation to a normal distribution could be attained by a logarithmic transformation (skewness = 0.02; kurtosis = 2.98) (see Fig. 4.2, bottom row). All successive analyses were therefore conducted on log-transformed data. For clarity, however, all

estimates will be reported here after an inverse anti-logarithmic transformation and will therefore be expressed in milliseconds. Thus, measures of central tendency are geometric means and confidence interval limits, which are symmetrical above and below the arithmetic mean on the log-scale, become asymmetrical after the inverse transformation but retain the standard interpretation.

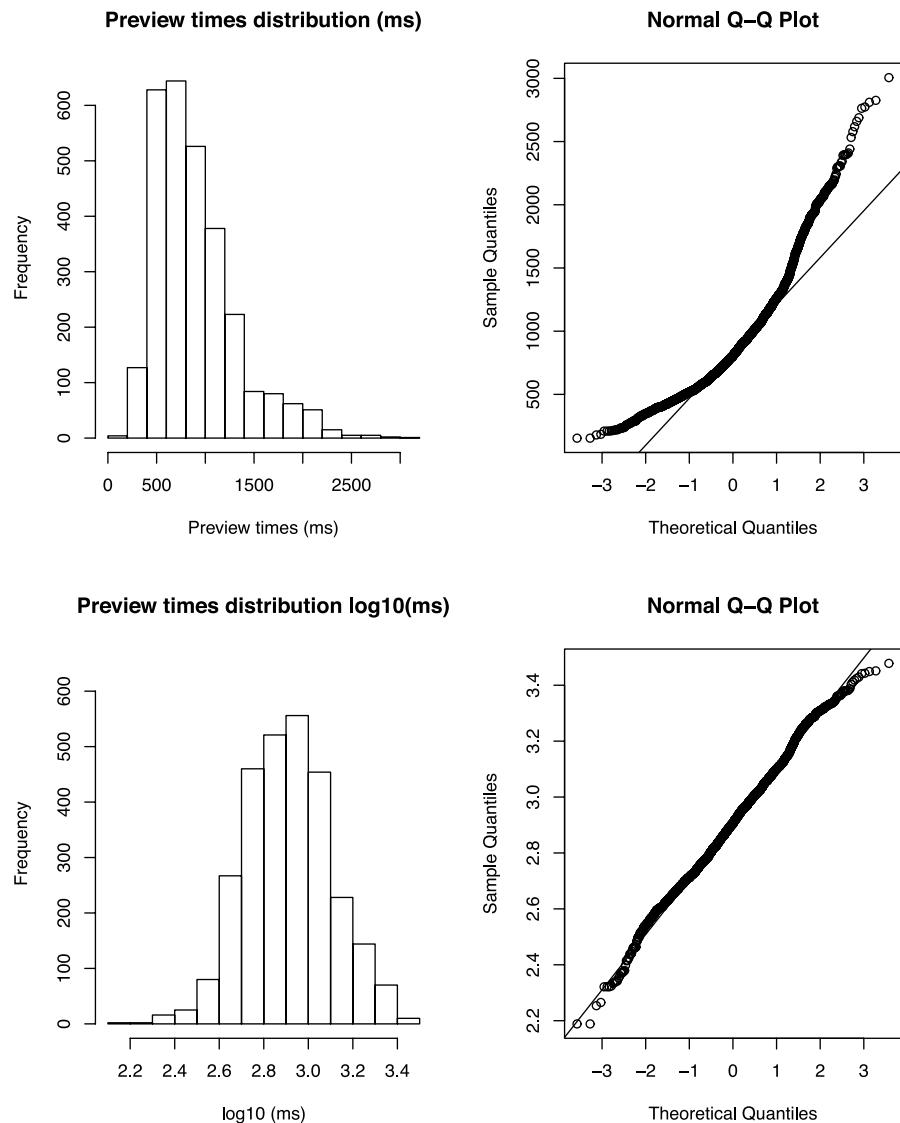


Fig. 4.2. Distribution of preview reaction times (PRT) in Experiment 1, before and after logarithmic transformation. Top row: Untransformed data. Bottom row: Data after logarithmic transformation. Top left: Histogram showing the positively skewed, leptokurtic PRT distribution. Top right: Normal quantile-quantile plot confirming

substantial deviations from normality. Bottom left: Histogram showing a better approximation to the normal distribution after transformation. Bottom right: Normal quantile-quantile plot. Histograms were binned following Sturges' rule (Sturges, 1926).

PRT results

PRT statistics for each condition are reported in Table 4.1. Fig. 4.3 presents geometric means for each participant as well as group averages in the baseline conditions. On average participants were faster (i.e., times were lower) when preparing pentapod grips (geometric mean 762 ms, 95% CI 735-790 ms) and slower when preparing pincer grips (805 ms, 776-834 ms) while tripod grips required an intermediate preparation time (785 ms, 758-813 ms).

PRT, log10(ms)		
condition	log mean, sd	geometric mean, 95%CI (ms)
10 10	2.906, .029	805 [776, 834]
35 10	2.939, .027	869 [841, 898]
120 10	2.953, .041	898 [854, 944]
35 35	2.895, .029	785 [758, 813]
10 35	2.907, .020	806 [786, 827]
120 35	2.912, .018	817 [799, 835]
120 120	2.882, .029	762 [735, 790]
10 120	2.895, .031	785 [756, 815]
35 120	2.888, .031	773 [744, 802]

Table 4.1. PRT statistics per condition, experiment 1.

To select the most appropriate model for our data, we fitted a multilevel linear mixed-effects model (LMM) with random intercept to our data using the *nlme* package in R (Pinheiro et al., 2017). The experimental condition (i.e., each distractor–target pair) was considered as the fixed factor. That is, instead of treating distractor and target as separate three-level variables, we treated each combination of the two as one level of the nine-level variable

“experimental condition”. The model with random intercept was chosen to account for the interindividual variability, so as to obtain estimates of fixed effect depured of individual differences. To justify this choice, we compared the fit of a generalized least squares (GLS) null model with fixed intercept (1) with that of a null model with random intercept (2) using a maximum likelihood criterion. Consistent with non-negligible individual differences in PRTs (as suggested by inspecting Fig. 3), the null model with random intercept proved superior than the null model with fixed intercept ($AIC(1) = 1221.227$, $AIC(2) = 5128.825$; likelihood ratio (1 vs 2): $\chi^2(1) = 3909.598$, $p < .0001$). The factor “experimental condition” was then added to model (2) as a fixed effect, generating model (3). The comparison with model (2) revealed that model (3) provided an even better fit ($AIC(3) = 5265.9$; likelihood ratio (2 vs 3): $\chi^2(5) = 153.087$, $p < .0001$), suggesting that times did not only vary between participants but were also modulated by the experimental condition.

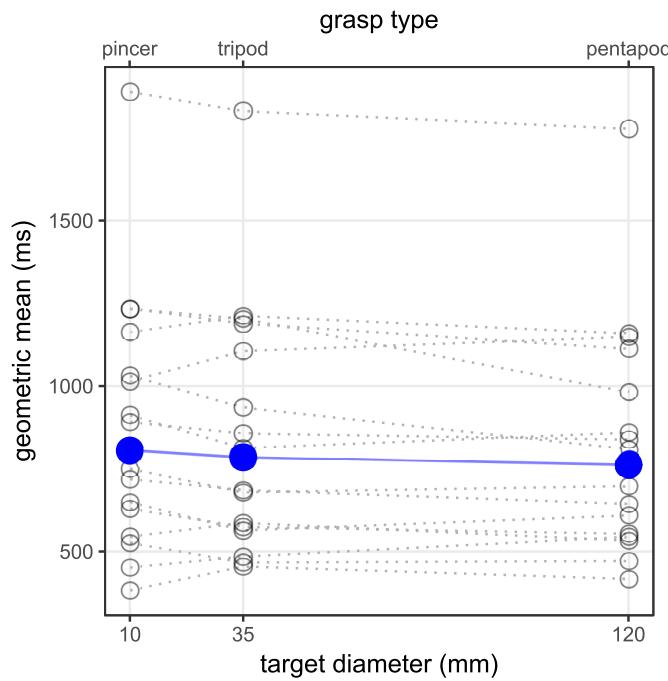


Fig. 4.3. Geometric PRT means in the baseline conditions (same distractor and target) of experiment 1. Filled circles: Group averages. Open circles: Individual means.

Given the outcome of our model selection, we used estimates from model (3) to compare the incongruent conditions with the corresponding baselines for each grasp type. That is, considering one grasp at a time, we compared times for grasping the target after the presentation of incongruent distractors to times associated with congruent distractor - target pairs. Fig. 4.4 presents maximum likelihood estimates of effects for each condition. Each plot refers to one of the grasp types, displaying estimates for each incongruent condition as well as their respective 95% confidence intervals (CI). Comparisons can be performed directly by evaluating whether these intervals cover the estimate for the appropriate baseline, which is marked by a vertical dotted line. These comparisons indicate that, although all incongruent pairs yielded times that were longer than their baselines, confidence intervals did not cover baseline estimates only in three out of six of the incongruent pairs. This occurred in both conditions associated to pincer grips (left panel), that is, after presentation of the large distractor (geometric mean 897 ms, 95% CI 867–927 ms) and of the medium distractor (869 ms, 840-899 ms), as well as in the condition associated with a tripod grasp after a large distractor (middle panel, bottom; geometric mean 817 ms, 790-845 ms).

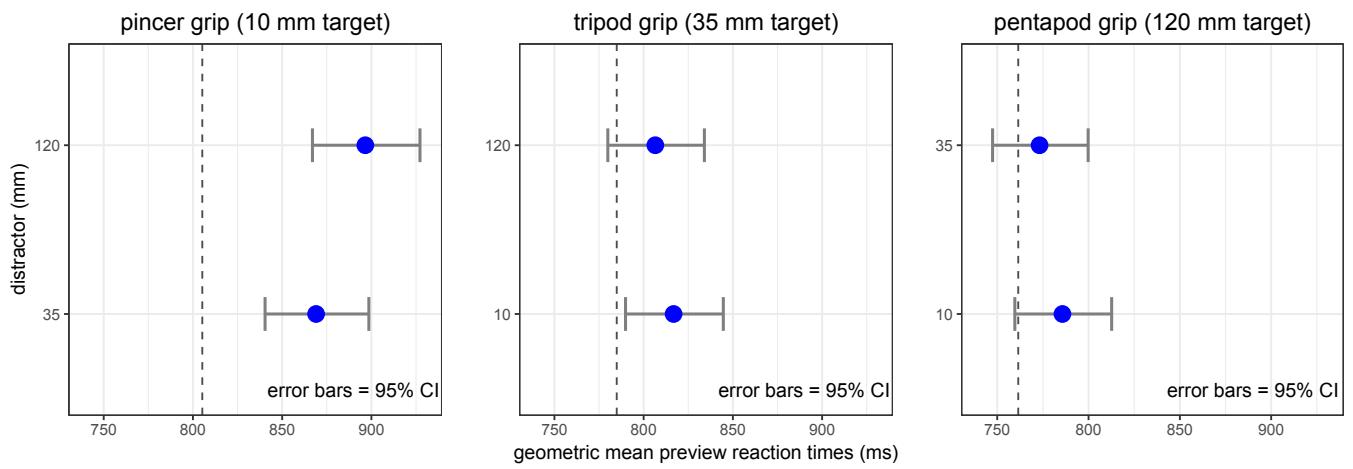


Fig. 4.4. Linear mixed model (LMM) estimates of effects of experimental conditions on PRTs, experiment 1. Each plot refers to a grasp type, displaying estimates for each incongruent condition. The dotted vertical line locates estimates for each

baseline condition. Error bars: 95% confidence intervals as calculated in the model. The LMM was fitted on log-transformed data; Estimates are reported as ms after the inverse anti-logarithmic transformation.

Maximum grip aperture

Kinematics data analysis and validation

Kinematics data for each trial were plotted and visually checked by the experimenters (V.P. and S.U.) to identify atypical grasping profiles and errors in the kinematics acquisition (e.g., lack of signal from one or more markers during the movement). After validation, a total of 33 trials (but only 5 tripod grips) were excluded from the MGA analysis. We therefore tested for the presence of extreme values in the MGAs distribution, using the same criterion employed in the PRT analysis:

$$\text{abs}(\text{MGA}-\text{median}(\text{MGA})) \geq 3 * \text{IQR}(\text{MGA})$$

That is, we preliminary estimated the median and interquartile range (IQR) of the MGA per target for each participant and then calculated the difference between the value and the median for each trial. Values with a difference from the median (in absolute terms) greater than or equal to 3 times the IQR were identified as outliers. A total of 30 trials (1.05% of valid trials) met this criterion and were excluded from further analyses.

MGA results

Fig. 4.5 summarizes mean MGAs for each type of grasp and target size within each participant, as well as the group averages. Finger apertures were scaled to the size of the target in each type of grasp. However, MGAs for grasping the small and medium disk were all larger than the physical size of the target, as expected for precision grips (for a review, see Smeets & Brenner, 1999) while MGAs for grasping the large target were close to the target size. This

feature of the data is consistent with a ceiling effect on MGAs associated to the largest target. MGA summary statistics for all conditions are presented in

MGA (mm)			
distractor	target	mean	95% CI
10	10	57.25	[53.49, 61.01]
35		57.32	[53.51, 61.12]
120		57.35	[53.51, 61.19]
35	35	77.43	[75.41, 79.44]
10		78.72	[76.42, 81.02]
120		76.44	[74.18, 78.69]
120	120	122.14	[118.02, 126.27]
10		121.71	[116.50, 127.05]
35		122.76	[118.68, 126.84]

Table 4.2. MGA statistics per condition, experiment 1.

Table 4.2. Given our hypothesis, we analyzed only grasps to the medium-sized target. As before, we used multilevel LMM with random intercepts to account for the interindividual variability in grip aperture and to obtain estimates of congruence effects depurated of individual differences. We preliminary compared the fit of a generalized least squares (GLS) null model with fixed intercept (1) with that of a null model with random intercept (2) using a maximum likelihood criterion. As for preview reaction times, the null model with random intercept provided a superior fit than the null model with fixed intercept ($AIC(1) = 6817.7$, $AIC(2) = 6127.5$; likelihood ratio (1 vs 2): $\chi^2(1) = 692.2$, $p < .0001$). The factor “distractor” was then added to model (2) as a fixed effect, generating model (3). The comparison with model (2) revealed that model (3) provided an even better fit ($AIC(3) = 6109.6$; likelihood ratio (2 vs 3): $\chi^2(2) = 21.9$, $p < .0001$), suggesting that grip apertures for the tripod grasp did not only vary between participants but were also modulated by the previously presented distractor. Fig. 4.6 shows the maximum likelihood estimates of effects calculated within model (3) as well as their respective 95% CIs. Estimates indicate that participants opened their fingers more after

the presentation of the small distractor (78.72 mm, 95% CI 77.77-79.67 mm) and less after the presentation of the large distractor (76.42 mm, 75.47-77.37 mm) and that both conditions are distinguishable from the same-distractor baseline (see error bars in the Figure 4.6).

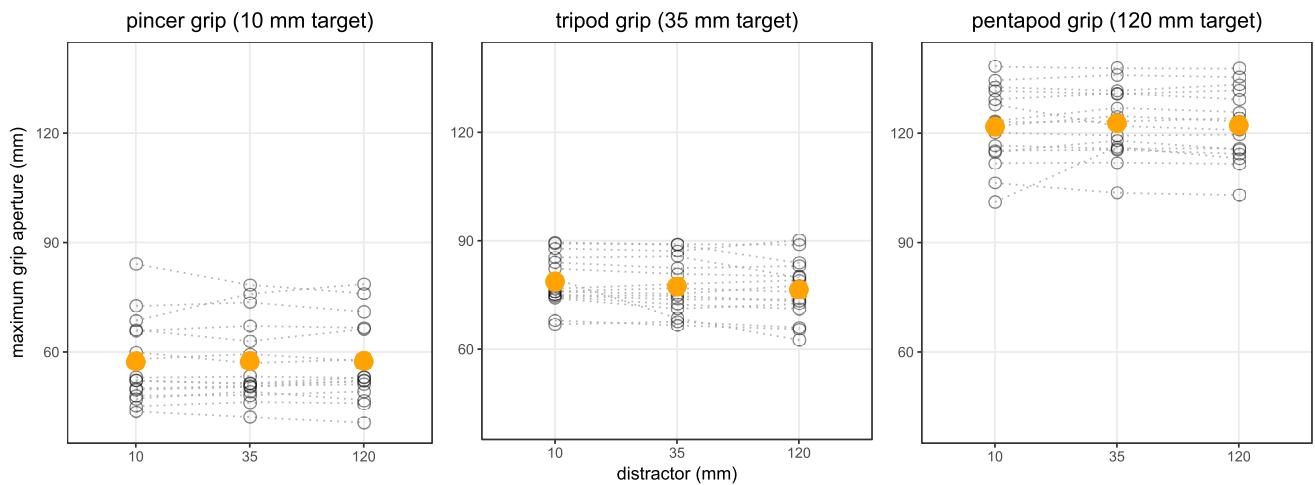


Fig. 4.5. Mean maximum grip aperture (MGA) when grasping the target for each type of grasp in experiment 1. Filled circles: MGA group averages. Open circles: Individual means.

Discussion

Preview reaction times

These results indicate that times when grasping targets varied depending on the previously presented distractor stimuli, in contrast to the predictions of the real-time programming hypothesis. In addition, as shown in Fig. 4.6, our results indicate that all estimates of effects for incongruent tests were larger than the corresponding baselines. This qualitative pattern is broadly consistent with the predictions of the visuomotor priming hypothesis. However, at least in the current study, costs were observed only in the conditions whereby the distractor was larger than the target stimulus. Specifically, greater costs were measured for pincer grips, when executed

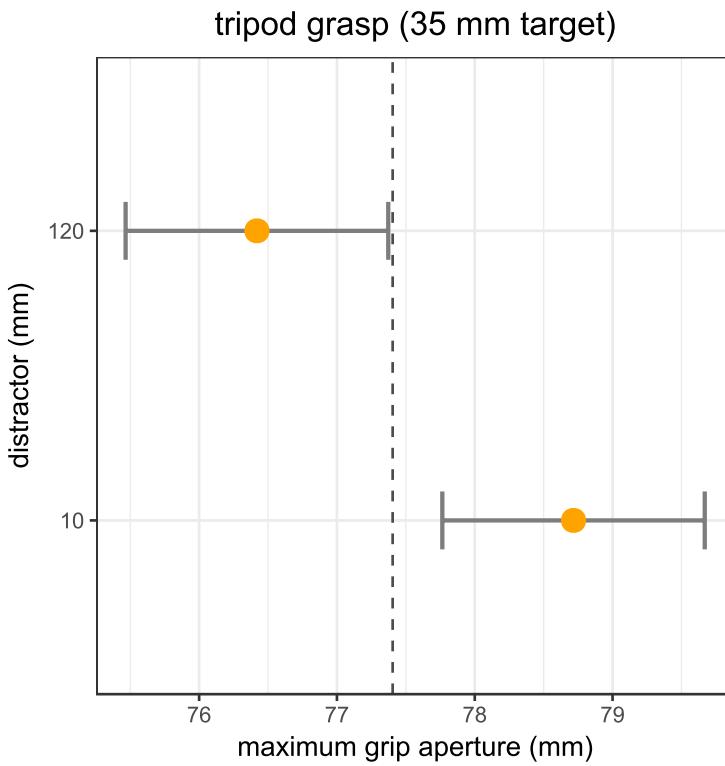


Fig. 4.6. LMM estimates of effects of experimental conditions on the MGA with tripod grasps, experiment 1. The dotted vertical line locates the estimate for the baseline condition (tripod grasp after viewing the 35 mm distractor). Error bars: 95% confidence intervals as calculated in the model.

after large or medium distractors, and for tripod grips when executed after large distractors. This pattern has two implications. First, it runs counter the predictions of finger-based visuomotor priming. According to this hypothesis (see introduction), grasps involving a smaller number of fingers should benefit, rather than suffer, from the implicit activation of grasps involving a larger number. Thus, the results should have been exactly opposite of what we observed. Second, this pattern suggests that other factors besides visuomotor incongruence may contribute to action planning. If visuomotor incongruence were the only factor responsible for longer times in our experimental conditions, relative to the corresponding baselines, none of the six confidence intervals should have covered the corresponding baseline means.

The hypothesis that best matches the current results is generalization of precision. As predicted by this hypothesis, we observed costs when participants grasped targets that were smaller than distractors (i.e., they presumably required a more precise motor program in comparison to that elicited by the distractor), but did not detect equivalent differences when participants grasped targets that were larger. These conclusions however are open to an objection. Although differences between incongruent conditions and baselines were observed only in the three cases predicted by generalization of precision, we did observe an overall cost on incongruent times in all six. At least qualitatively, this outcome is consistent with visuomotor priming and it is possible, in principle, that the sample size employed in the current study was not adequate to corroborate this pattern also quantitatively (i.e., to estimate sufficiently narrow confidence intervals). In addition, the design of the current experiment focused on comparisons between congruent (taken as baselines) and incongruent distractor-test pairs. Because it lacks a no-distractor control to assess benefits as well as costs, this design provides a sub-optimal test for a priming mechanism. A no-distractor control is needed especially because baseline times varied between the three types of precision grips. For instance, motor preparation was shorter for pentapod in comparison to pincer grips. Given that this advantage would apply also to the incongruent trials, it is possible that this reduced the observed cost, making it harder to detect reliably. To tackle this and related issues, we conducted a second experiment adopting an improved design.

Maximum grip apertures

These results indicate that the aperture of the index and thumb when performing tripod grasps was modified, in comparison to same-distractor baselines, by previously presented, irrelevant incongruent distractors. Specifically, when the mid-size target was preceded by a larger distractor, the aperture was reduced in comparison to the baseline. Conversely, when the mid-size target was preceded by a smaller distractor, the aperture was

enlarged. The observation of an effect of size contrast on grasping runs counter the predictions of the TVSH.

Remarkably, the effect size observed in the current study was very similar to the equivalent statistic observed in our previous paper (Uccelli et al., 2019). Specifically, Uccelli and collaborators observed average differences in the MGA after larger and smaller distractors of the order of 2.8% of the diameter of the target, whereas in the current study the corresponding statistics was about 2.9%. Thus, these results are fully consistent with our previous findings that sequential size contrast can modulate the interdigit aperture in grasping (Uccelli et al., 2019). That the effects are so similar across the two studies is all the more remarkable given the differences in the tasks. In our earlier study participants grasped intermediate-size targets using pincer grips. Thus, the maximum grip aperture captured the size-dependent scaling of finger aperture in full. In the current study, instead, participants responded with tripod grasps but we recorded the kinematics of only two of the three fingers involved. As a consequence, the customary maximum aperture measure may have reflected only one component of the scaling of interdigit distances. Although we did not test this issue directly, the current results suggest instead that the thumb-index aperture is informative about size-scaling even in tripod grasps. This is consistent with earlier reports that the index and middle finger move in consort during a tripod grasp (Gentilucci et al., 2003), yielding correlated kinematic markers.

Experiment 2

We introduced two changes in the experimental design of the first experiment. One was merely a simplification, aimed at better revealing potential differences. To achieve this goal, we dropped all conditions involving tripod grasp and focused on the comparison between the pincer and the pentapod. The other, and more critical, change was the addition of a no-distractor

baseline. Preview reaction times associated with such baselines are informative about the preparatory phase of each type of grasp, based only on visual information about the target and nothing else. According to the visuomotor priming hypothesis the previous presentation of a same-size (i.e., congruent) distractor should produce a benefit (i.e., shorter times relative to baseline), whereas the previous presentation of distractors having different sizes from the target should produce costs (longer times). Thus, relative to the no-distractor baseline we would expect pincer grips after small distractors, and pentapod grips after large, to yield reliably shorter times. Conversely, we would expect pincer grips after large distractors, and pentapod grips after small, to yield reliably longer times. According to the generalization of precision hypothesis a different pattern is instead predicted. In this proposal, a more precise motor plan should generalize to grasps requiring a less precise one, whereas a less precise plan should not. Thus, relative to the no-distractor baseline, we would expect pentapod grips following small distractors to be facilitated, and pincer grips following large distractors to remain unaffected or to suffer a delay in preparation if the new computation of the motor program requires to first erase the program evoked by the distractor. Relative to the appropriate congruent conditions (i.e., the baseline of the previous experiment), instead, we expect to see again slower preparation times for pincer grips following large distractors, but no difference in preparation times for pentapod grips following small distractors.

Methods

Participants

We recruited 16 participants (9 females and 7 males; age range 23-31) from the University of Parma community. All were right-handed, had normal or corrected-to-normal eyesight, no history of neurological diseases and were unaware of the purpose of the study.

Design

The design of the experiment resulted from crossing distractors and targets as within-participant independent variables. We used two disk sizes (small and large) as targets, and the same disks as distractors plus a no-distractor baseline. This led to a total of 6 conditions, of which 2 were baselines (no distractor), 2 were congruent (same size and same associated grasp for distractor and target stimuli), and 2 incongruent (different size, different grasp). Each condition was presented 20 times in randomized order, totaling 120 trials.

Results

We performed the same analysis as in the first experiment.

Preview reaction times

PRT data analysis and validation

The time from one of the trials was lost due to a technical problem. This trial was discarded from the overall sample. Using the same criteria as in experiment 1, we tested for the presence of extreme values in the preview distribution (see experiment 1 results section). A total of 4 trials were identified as anticipatory responses and 24 trials were identified as outliers. Overall, 28 trials (1.46% of the total of valid trials) were discarded.

We then proceeded by checking the overall distribution. The distribution was slightly asymmetrical (skewness = 0.47) and mesokurtic (kurtosis = 3.06), as shown in Fig. 4.7 (top row). Thus, times were again positively skewed, but less so than in Experiment 1. This outcome suggests that a transformation of these times is not strictly needed to meet the standard assumptions for inferential analysis. In accord with this impression, after a logarithmic transformation (Fig. 4.7, bottom row) the distribution was still skewed, but negatively instead of positively (skewness = 0.71; kurtosis = 3.12). Given this difference relative to distributions observed in the previous study, we conservatively decided to perform equivalent analyses of both the

untransformed times and of the log-transformed times. Because these two analyses yielded exactly the same pattern of results, for consistency with the previous experiment here we will report the analysis on the log-transformed times. Thus, as for the previous experiment measures of central tendency are geometric means of preview time and confidence intervals are derived from the antilogarithms of the upper and lower limits computed on the log-transformed data.

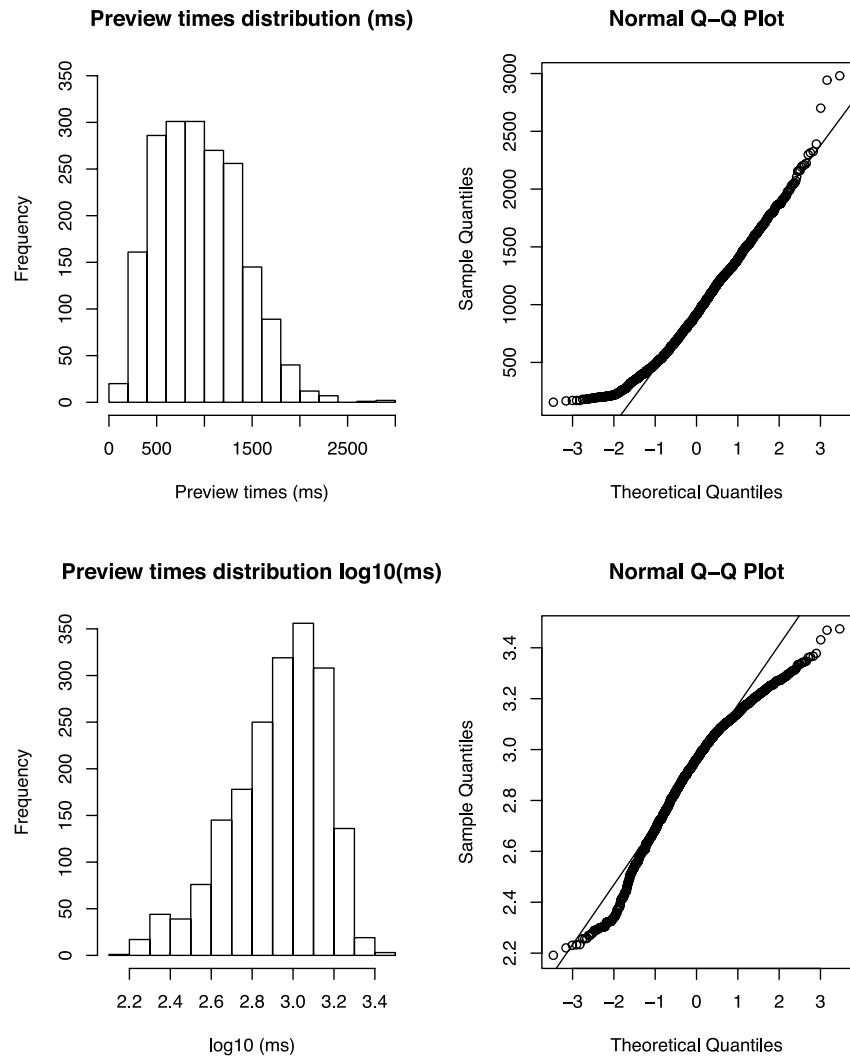


Fig. 4.7. PRT distribution in Experiment 2, before and after logarithmic transformation. Top row: Untransformed data. Bottom row: Data after logarithmic transformation. Histograms binned following Sturges' rule (Sturges, 1926).

PRT results

PRTs for each condition are reported in Table 4.3. Fig. 4.8 presents geometric PRT means for each participant as well as group averages in the no-distractor baseline and in the incongruent conditions. In the baseline conditions on average participants were faster (i.e., times were lower) in performing pentapod grips (geometric mean 796 ms, 95% CI 761-834) and slower in performing pincer grips (890 ms, 850-931 ms). Pentapod grips (786 ms, 757-816 ms) were also faster than pincer grips (867 ms, 837-898 ms) in the congruent conditions. This pattern replicates the advantage in preparing pentapod grips relative to pincer grips that we observed in the first experiment. Following the same procedure as in experiment 1, we fitted a multilevel LMM with random intercept (again using nlme in R). The experimental condition (i.e., each distractor/no distractor - target pair) was considered as the fixed factor. The model with random intercept was chosen to account for interindividual variability, so as to obtain estimates of fixed effect depured of individual differences. To justify this model, we proceeded as in experiment 1. Thus, we first compared the fit of a generalized least squares (GLS) null model with fixed intercept (1) with that of a null model with random intercept (2) using a maximum likelihood criterion. Consistent with non-negligible individual differences (as suggested by Fig. 4.8), the null model with random intercept provided a better fit than the null model with fixed intercept (AIC (1) = 191.688, AIC(2) 1/4 3400; likelihood ratio (1 vs 2): $\chi^2(1) = 3211.236$, $p < .0001$). The factor “experimental condition” was then added to model (2) as a fixed effect to generate model (3). Compared to model (2), model (3) revealed an even better fit (AIC (3) = 3592.483; likelihood ratio (2 vs 3): $\chi^2(5) = 201.559$, $p < .0001$), suggesting that times not only varied between participants, but were also modulated by the experimental condition. Fig. 4.9 presents maximum likelihood estimates of effects in the congruent and incongruent conditions, within model (3).

PRT, log10(ms)		
condition	log mean, sd	geometric mean, 95%CI (ms)
<i>pincer baseline</i>	2.949, .037	890 [850, 931]
10 10	2.938, .029	867 [837, 898]
120 10	2.969, .036	930 [890, 972]
<i>pentapod baseline</i>	2.901, .037	796 [761, 834]
120 120	2.895, .031	786 [757, 816]
10 120	2.886, .034	770 [738, 803]

Table 4.3. PRT statistics per condition, experiment 2.

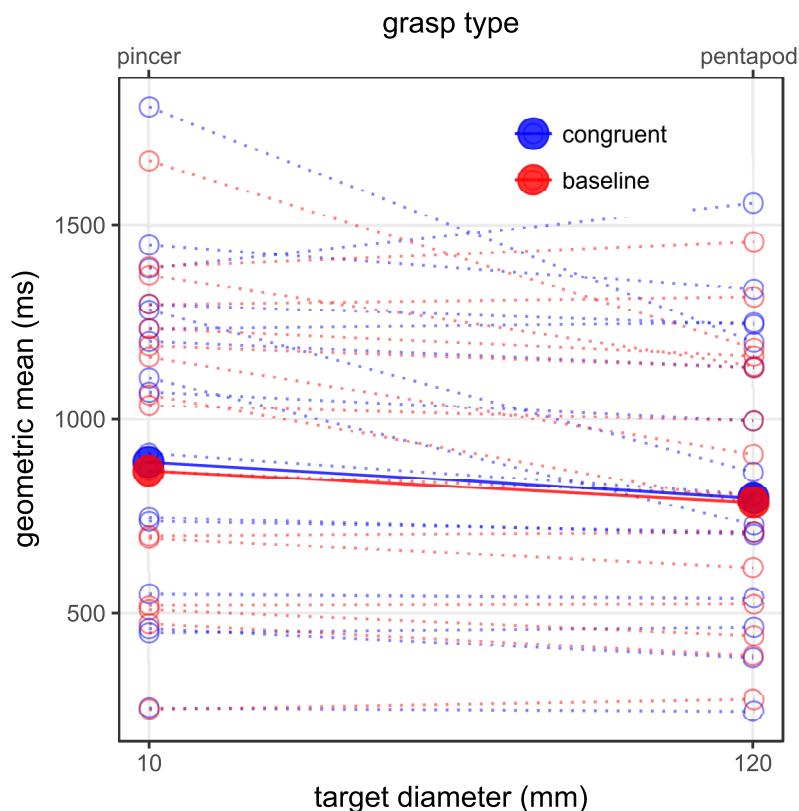


Fig. 4.8. Geometric PRT means in the baseline (red) and congruent (blue) conditions in experiment 2. Filled circles: Group averages. Open circles: Individual means.

Preview reaction times before performing a pincer grip were higher than the baseline in the incongruent condition, that is, with the large distractors (geometric mean 930 ms, 95% CI 901-961 ms). In the congruent condition (small distractor) pincer grip times were instead lower than the baseline (897 ms, 839-895 ms), but this difference was not reliably different from baseline (see upper limit of the CI). For the pentapod grip, times in the incongruent condition (small distractor) were instead lower than the baseline (770 ms, 745-796 ms), while in the congruent condition they were not reliably different from baseline (785 ms, 760-811 ms). In summary, both incongruent conditions were reliably different from the corresponding no-distractor baselines, but these effects were in opposite directions: large distractors caused an increase in times for grasping small targets with a pincer grip, whereas small distractors facilitated grasping large targets with a pentapod grasp.

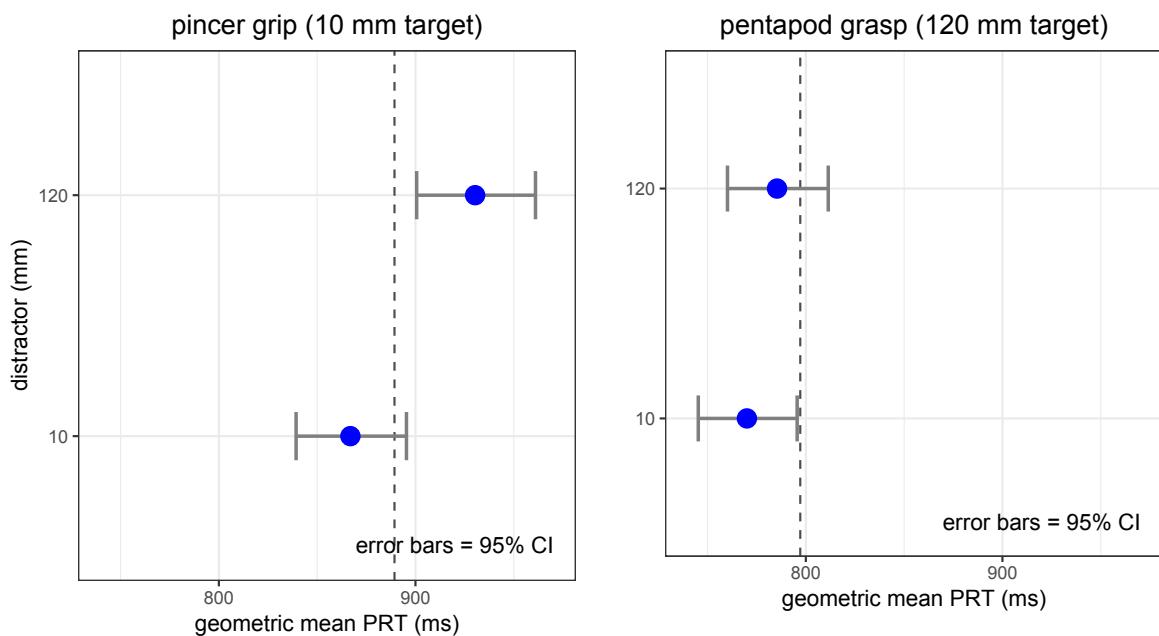


Fig. 4.9. LMM estimates of effects of experimental conditions on PRTs, experiment 2. The dotted vertical line locates estimates for each baseline (note that now baselines are no-distractor conditions). Error bars: 95% confidence intervals as calculated in the model. The LMM was fitted on log-transformed data; Estimates are reported as ms after the inverse anti-logarithmic transformation.

Maximum grip aperture

Kinematics data analysis and validation

After validation, a total of 38 trials were deemed invalid (due to lack of signal from one or more markers during the movement) and were removed from the overall sample. A total of 41 trials (2.18% of valid trials) were identified as outliers and subsequently excluded from the MGA analysis. Overall, a total of 17 baseline trials were discarded.

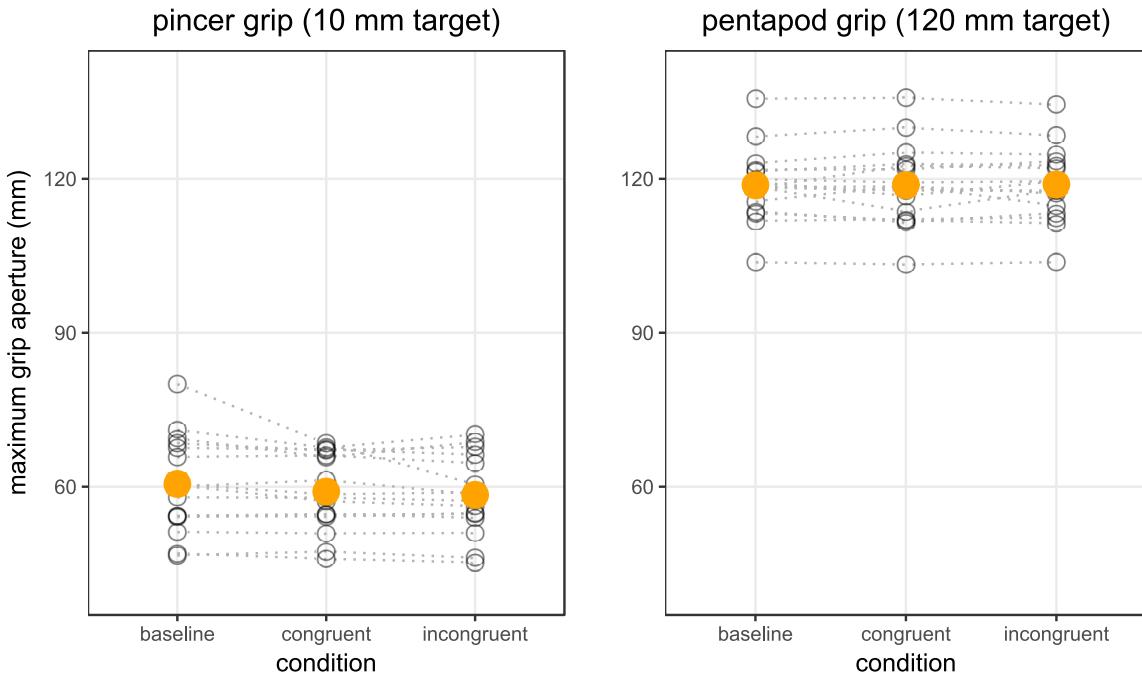


Fig. 4.10. Mean maximum grip aperture (MGA) when grasping the target for each type of grasp in experiment 2. Filled circles: MGA group averages. Open circles: individual means.

Maximum grip aperture results

Fig. 4.10 summarizes the MGA results for each type of grasp and target size along with the group averages in the baseline trials (no distractor conditions) and in the congruent trials. Overall, finger apertures were scaled to target size

as expected. Also as expected, MGAs associated to pincer grips were larger than the physical size of the target in both conditions (grand mean 60.54 mm, 95% CI 57.22-63.85 mm; 59.04 mm, 56.31-61.78 mm, respectively), and similar to the baseline MGA from the first experiment (57.25 mm, 53.49-61.01). Conversely, MGAs associated to pentapod grasps were smaller than the target size both in the baseline and in the congruent condition (118.82 mm, 116.16-121.47 mm; 118.77 mm, 116.16-121.47 mm, respectively). These results confirm our previous suspicion that MGA when grasping the large targets were compressed due to a ceiling effect. For both pincer and pentapod grips, participants' MGAs in the congruent and incongruent conditions were essentially the same. Thus, as in the first experiment, results do not suggest the presence of any effect of the previously presented distractor on pentapod and pincer grips.

Discussion

The aim of our second experiment was to compare visuomotor priming and generalization of precision by means of a design that implies clearly different patterns of costs and benefits on preview reaction times. In comparison with the respective baselines we observed a cost on preview reaction times for incongruent pincer grips, but a benefit for incongruent pentapod grasps. Although the former of these results is consistent with the predictions of a visuomotor priming mechanism, the latter is in fact in the opposite direction to that predicted by visuomotor priming. In addition, we failed to observe benefits in the congruent conditions with both types of response, although there was a trend for both averages to be slightly slower than their respective baselines. Thus, both qualitatively and quantitatively, the observed pattern of results is at odds with visuomotor priming, whereas it corresponds well with expectations based on generalization of precision.

General discussion and conclusions

Our findings support the automatic visuomotor coding hypothesis. Specifically, our two experiments provide support for the hypothesis that a distractor stimulus can activate an implicit motor representation for grasping it and that this process is obligatory as distractors were irrelevant to our task. Thus, motor representations elicited by an implicit preparatory process can interact with motor representations involved in planning a subsequent actual grasp on a different object. These findings are instead at odds with a null, no effect hypothesis as predicted by the real-time view (Milner and Goodale, 2006; Westwood and Goodale, 2003).

The pattern of costs and benefits on preview reaction times indicate that the effect of implicit preparation is not a form of priming. We considered two possible such forms, visuomotor priming as reported by Craighero et al. (1998), and finger-based visuomotor priming. The distinction between these two forms of priming is interesting, because it has been argued that the form of priming reported by Craighero and by others may not reflect interactions between dorsal, object-directed motor processes but memory-guided actions which recruit representations coded by the ventral stream, that is, of interactions that are not truly visuomotor in the real-time view of dorsal processing (Cant et al., 2005). Therefore, evidence of this form of priming may have been ambiguous in relation to the real-time view. Finger-based visuomotor priming, in contrast, represents a putative process that involves true motor parameters, such as the trajectories of individual fingers. Therefore, evidence of this other form of priming may have been informative in relation to the real time view. Neither hypothesis however proved successful in predicting our pattern of results. Interestingly, the hypothesis that best predicted our results is generalization of precision.

A possible neural mechanism underpinning this process may be surround inhibition in the motor system (for a review, see Beck & Hallett, 2011). In

surround inhibition, fine tuning of neuronal activation related to specific stimulus features is achieved by the concurrent suppression of adjacent neurons. It has been reported that a similar mechanism may underlie skilled motor behavior as, for instance, individuated finger movements. For instance, inhibition of adjacent non-involved areas has been observed in primary motor cortex (Beck & Hallett, 2011; Sohn & Hallett, 2004). On the basis of surround inhibition in motor areas, one would expect that pincer, tripod, and pentapod grips require inhibition of three, two, or no fingers, respectively. Thus, there may be a specific relationship between motor precision and surround inhibition, in that an increase in inhibition would be required to perform more precise movements. In our experiment, grasps involving a smaller number of fingers than those implicitly pre-activated from seeing the distractor would require inhibition of the uninvolved fingers. Conversely, grasps involving a larger number of fingers would need no equivalent inhibition, but may instead “inherit” the precision setting evoked by seeing a smaller distractor. It is therefore possible to argue, at least speculatively, that generalization of precision may be implemented within a neural network by a surround inhibition mechanism. This speculation will need further testing within experimental designs that can disentangle the effects of the number of fingers involved in each motor representation from the effects of stimulus size as a determinant of sensorimotor precision.

In conclusion, note that precision – as a motor parameter – has little to do with the semantics of object representations but plays a key role in the preparatory computations for object-directed grasps. For this reason, we suggest that our results are consistent with a truly visuomotor process within the dorsal stream and reveal a form of temporal interaction between implicit and explicit motor processes. A potential limitation of this interpretation of the current findings is that our dependent measure (the preview reaction time) was under the control of participants and may therefore reflect only deliberate, conscious motor programming rather than motor preparation in general. Consistent with this possibility, we note that our measured preview reaction times were overall

fairly large, often still within the range of typical choice reaction times but at times larger than that (and we had one participant with average times of about 1.5 s, which is unusually large). If this concern is correct, one of the implications of the current findings – evidence against dorsal amnesia – may be weakened by the possibility that faster, or more reactive motor preparation would show a different pattern of results. This is an empirical question that we plan to address in future contributions to the literature.

Chapter 5

Asymmetric effects of graspable distractor disks on motor preparation of successive grasps: A behavioural and event-related potential (ERP) study

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Abstract

There is evidence that seeing a graspable object automatically elicits a preparatory motor process. However, it is unclear whether this implicit visuomotor process might influence the preparation of a successive grasp for a different object. We addressed the issue by implementing a combined behavioural and electrophysiological paradigm. Participants performed pantomimed grasps directed to small or large disks with either a two (pincer) or a five-finger (pentapod) grip, after the presentation of congruent (same size) or incongruent (different size) distractor disks. Preview reaction times (PRTs) and response-locked lateralized readiness potentials (R-LRPs) were recorded as online indices of motor preparation. Results revealed asymmetric effects of the distractors on PRTs and R-LRPs. For pincer grip disks, incongruent distractors were associated with longer PRTs and a delayed R-LRP peak. For pentapod grip disks, conversely, incongruent distractors were associated with shorter PRTs and a delayed R-LRP onset. Supporting an interpretation of these effects as tapping into motor preparation, we did not observe modulations of stimulus-locked LRP's (sensitive to sensory processing), or of the P300 component (related to reallocating attentional resources). These results challenge models (i.e., the "dorsal amnesia" hypothesis) which assume that visuomotor information presented before a grasp will not affect how we later perform that grasp.

Introduction

We effortlessly grasp objects many times every day, but grasping involves non-trivial problems of motor control. For instance, the hand must be configured before contact, and in this a key role is played by the object size as this critically constrains which fingers will be involved. For a small object, such as a peanut, we will typically use a thumb-index opposition grip ('pincer grip'). For a larger object, such as an apple, we will instead use all five fingers, with the thumb opposing the other four ('pentapod grip'). In both cases, however, the hand will approach the object quickly, open the required amount, and finish the movement by closing the digits on the aimed contact points on the object (Jeannerod, 1981; Marteniuk et al., 1990). Despite a large literature (see Smeets et al., 2019), preparatory processes involved in this remarkably efficient motor behavior are not fully understood. For instance, it is un-clear whether a first motor representation can affect a second, successive motor program. Using a sequential paradigm, we investigated whether, and how, a first motor representation elicited by a graspable object affects the preparation of a second motor program aimed at grasping a different object. The theoretical backdrop of our research question lies in two concepts: affordances and visuomotor priming.

The term *affordance* (Gibson, 1979) refers to the direct perception of potentialities for action. Although the notion has been debated (de Wit et al., 2017; Chong & Proctor, 2020), a common prediction is that object observation activates motor representations even if no action will be carried out. Viewing a graspable object, for instance, automatically activates an internal representation of the potential grasp. Evidence supporting this prediction is provided by studies on monkeys (Jeannerod et al., 1995; Murata et al., 1997; Maranesi et al., 2014), as well as behavioural (Chao & Martin, 2000; Tucker & Ellis, 1998, 2004), imaging (Anderson et al., 2002; Grèzes & Decety, 2002), and TMS (Buccino et al., 2009; Grèzes et al., 2003) studies on humans. However, this literature is not directly concerned with the issue of possible

effects of such representations on subsequent performed actions. Evidence relevant to this issue is instead provided by visuomotor priming tasks (Craighero et al., 1996; Craighero et al., 1998). In these tasks, reaction times are shorter (i.e. benefits) or longer (i.e. costs) depending on whether a feature of the target stimulus (e.g., its orientation) is congruent or incongruent with the corresponding feature of an initial prime (see Craighero et al., 1996, 1998). Similar findings have been replicated and extended in other studies (Hesse et al., 2008; Roche & Chainay, 2013; Seegelke et al., 2016). It has also been argued, however, that visuomotor priming effects may not occur at the level of motor representations and could well involve semantic rather than motor interactions (Cant et al., 2005; but see, Hesse et al., 2008, Seegelke et al., 2016).

Thus, empirical work on affordances and on visuomotor priming indicates that a motor representation might be automatically elicited when seeing an object that affords appropriate action potentialities. We call this the *automatic visuomotor encoding* hypothesis. However, it remains unclear whether such representations can feed later motor processes. For instance, they might be confined to the seen object in space and especially in time, such that they will quickly decay as soon as new processing is called for. Indeed, it has been proposed that object-directed actions rely only on online sensory information. This *real time motor control* view (Westwood and Goodale, 2003) is a key feature of the influential two-visual-systems hypothesis (TVSH, Goodale and Milner, 1992; Milner and Goodale, 2008; Milner, 2017). According to the TVSH, the ventral stream codes visual information to generate representations that remain invariant under contextual changes allowing object recognition (“vision-for-perception”). Instead, the dorsal stream processes information relevant for the online control of goal-directed actions (“vision-for-action”). Critically for the purposes of the current paper, vision-for-action is assumed to code “here-and-now” relationships between an object and the action’s effector, disregarding how the object relates to its context, especially in time (i.e., “dorsal amnesia”; Schenk and Hesse, 2018).

In this paper, we challenged real time motor control investigating whether motor preparation for grasping an object is affected by a previously elicited motor representation for grasping a different object. Imagine the following situation. You see a peanut. Immediately afterwards, you see an apple, which you have to grasp. Will the peanut (which affords a *pincer* grip), affect the motor preparation for grasping the apple (which affords a *pentapod* grip)? If object observation automatically elicits an (implicit) motor representation (i.e., if there is automatic visuomotor encoding), one could expect that this representation might affect the successive action. Support for this prediction is provided by a study on the Uznadze illusion in action (Uccelli et al., 2019). In this illusion, the same object is perceived as smaller when preceded by a larger object and vice versa (Uznadze, 1966). This temporal size contrast yields strong perceptual effects in haptics (Kappers & Bergmann-Tiest, 2014), in vision-for-perception (Bruno et al., 2018), and in a vision-for-action task (Uccelli et al., 2019).

Critical for the purpose of the current paper, there is evidence that the effect of the Uznadze illusion might already occur at the level of motor preparation (Pisu et al., 2020). In this work, small, medium, and large disks were used both as distractors and as targets. Small disks were associated with ‘pincer grips’ (thumb-index opposition), medium disks with ‘tripod grips’ (thumb vs index and middle), and large disks with ‘pentapod grips’ (all five fingers). The design involved congruent (baseline) or incongruent (differently sized targets and distractors) conditions. After seeing a distractor, participants grasped a target in open-loop conditions after a discretionary preview time window. This determined the preview reaction time (PRT), i.e. the time spent observing the target before movement onset. Results indicated that incongruent distractor-target pairs were generally associated with longer PRTs, but differences were reliable only when participants grasped small targets after the presentation of larger distractors. When large targets were grasped after the presentation of smaller distractors, PRTs could not be reliably differentiated from the relevant baseline. Pisu et al. (2020) interpreted this pattern as reflecting an asymmetric

generalization of precision between the two motor programs. They suggested that the implicit pre-activation of less precise grips (i.e., pentapod) yielded longer PRTs as the precision parameter had to be updated to perform a more demanding grip (i.e., pincer). Conversely, the higher precision associated with a pincer grip generalized to the preparation of a successive, less precise grip. Here we sought to corroborate this interpretation by investigating into the temporal dynamics of brain activity related to the preparation of grasping.

Testing real-time control with ERPs: rationale and predictions

Components of ERPs can provide temporal markers for specific brain processes. In motor preparation, one such marker is the lateralized readiness potential (LRP). The LRP is a slow negative ERP modulation which unfolds well before movement initiation from one of the motor cortices (Gratton et al., 1988; Smulders & Miller, 2012). LRPs can be measured with reference to stimulus onset (stimulus-locked lateralized readiness potential, or S-LRP), or to action initiation (response-locked, or R-LRP). The former reflects stimulus processing, while the latter reflects motor preparation (Smulders & Miller, 2012; Leuthold et al., 1996; Osman et al., 1992). In addition, stimulus processing in preparation for an action recruits attentional resources. The P300 is a positive ERP component that appears after a task-relevant stimulus (Sutton et al., 1965). Although the issue is still debated (Verleger, 1997), P300 amplitude is generally believed to reflect “context updating” in terms of attentional costs (Donchin & Coles, 1988), while P300 latency (i.e., the time between stimulus onset and P300 amplitude peak) is believed to reflect evaluation and categorization processes, independent of response selection and execution (Segalowitz et al., 1997; Magliero et al., 1984).

By using LRPs, we aimed to extend previous work on temporal dynamics within cortical networks for motor preparation. Specifically, we aimed to assess how an implicit motor representation might affect the preparation of an explicit successive grasp. If PRTs for grasping a target are modified by the presentation of incongruent distractors (as reported by Pisu et al., 2020), and

if this effect occurs at the level of motor preparation (as hypothesized again by Pisu et al.), then corresponding ERP modulations should be observed in R-LRP's, but not in S-LRP or P300 components.

Methods

Power analysis

To determine the adequate sample size, we conducted an a-priori power analysis. First, we asked what would be a meaningful effect size for the present research. Pisu et al. (2020) reported that non-transformed PRTs group averages of 16 participants in the baseline (congruent) conditions were 890 and 830 ms for pincer and pentapod grips, respectively. In the corresponding test (incongruent) conditions, group averages were 990 and 860 ms (i.e., incongruent distractor-target pair of disks revealed effect sizes of ≈ 100 and 30 ms). Taking these results as a starting point, we assessed power under three hypothetical scenarios involving effect sizes equal to 70%, 60%, or 50% of effects found by Pisu and colleagues. Power estimates were obtained by simulating and then modelling 10,000 independent experiments using the *simr* package in R (Green & MacLeod, 2016), with increasing numbers of participants. We selected $n = 22$ as power estimates were 0.99, 0.95, and 0.85 for the three scenarios, respectively. Finally, we assumed that this sample size would be adequate to detect differences in ERP signatures as there is no a-priori reason to predict larger inter-participant variability than in PRTs, especially given that we registered LRP signals in 60 trials for each experimental condition when it is usually recommended that 40-50 trials suffice to derive satisfactory waveforms (Eimer, 1998). Details of the power simulations are provided in the Open Analysis document (<https://osf.io/yvsg5/>).

Participants

Twenty-two members of the Liverpool Hope University community (9 females and 13 males, mean age = 23.9, range: 19-37) participated. All were right-handed, had normal or corrected-to-normal vision, no history of neurological disease, and were unaware of the purpose of the study. Seventeen undergraduate students volunteered by booking weekly slots on the SONA recruitment system and received course credits for participating in the study; the other five were faculty members of the Department of Psychology recruited by the first author. The only inclusion criterion was that they be right-handed. One additional volunteer was excluded from the analysis as she turned out to be left-handed after testing had already been completed.

Ethics

All participants signed a written informed consent form before participating and were debriefed as to the purposes of the study after participation. The study received approval from the Psychology Research Ethics Committee of Liverpool Hope University and was conducted in accordance with the ethical standards of the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki), as well as the Code of Ethics and Conduct of the British Psychological Society.

Stimuli

Stimuli were generated in MATLAB (2015b, The MathWorks, Natick, MA, USA) using the Psychophysics toolbox extension, version 3.0 (Brainard, 1997). They consisted of a small and a large white disk having diameters of 38 and 380 pixels, respectively (corresponding approximately to 10 and 100 mm). They were presented at the center of the computer screen surrounded by a black background. The on-screen luminance of the disks and background were approximately 95 and 0.5 cd/m². Stimuli were presented on a 17 in. monitor controlled by a computer running the Windows XP operating system.

Task

Participants pantomimed a reach-to-grasp movement with their right hand towards a small or large target disk, after a discretionary preview time window. Disks were paired with a different type of grasp, considered as the most appropriate grasp for an object having that size. Pairings were defined based on the taxonomy proposed by Feix et al. (2015). Thus, participants were instructed and trained to grasp the small disk with a pincer grip (thumb and index opposition) and the large disk with a pentapod grip (all five fingers).

Design

The design resulted from crossing two within-participant independent variables: the distractor (two levels, see Stimuli section) and target (also two levels) sizes. This yielded four experimental conditions, each consisting of one distractor-target pair. Two of these pairs involved distractors and targets having the same size (congruent, baseline). The other two involved distractors and targets having different sizes (incongruent, test). The experimental design is illustrated in Fig. 5.1. Given our rationale, we compared each incongruent pair with its appropriate baseline. Thus, we compared responses to small targets preceded by large distractors to the baseline involving small targets preceded by small distractors. Similarly, we compared responses to large targets preceded by small distractors to baselines involving large targets preceded by large distractors. To minimize participant fatigue, the experiment was divided into 6 blocks separated by 2-3 min pauses, giving the participant a brief break while the experimenter prepared the next block. Each pair was presented 10 times, yielding a total of 40 fully randomized trials per block. Thus, over the 6 blocks we collected measures from 240 trials, (60 distractor - target trials per pair per participant).

		distractor (mm)	
		pincer grip	pentapod grip
		10	100
target (mm)	pincer grip		
	●	congruent (baseline)	incongruent (test)
	10		
target (mm)	pentapod grip	incongruent (test)	congruent (baseline)
	100		

Fig. 5.1. The four experimental conditions. Participants were trained to perform a simulated pincer (index-thumb opposition) or pentapod (thumb - other four fingers) grip, respectively on a small (10 mm diameter) or large (100 mm diameter) target disk. Congruent or incongruent distractors were presented before tests.

Procedure

The participant sat on a comfortable chair in a lightly lit room. A keyboard was placed on the table in front of the participant. The center of the spacebar and the participant's midline were aligned with the center of the computer screen. The spacebar was placed at exactly 23 cm from the computer screen, corresponding to a viewing distance of approximately 50 cm. The experiment began with a verbal explanation, followed by twelve randomly chosen practice trials. When necessary, practice trials were repeated additional times until the participant was comfortable with the trial sequence. A written reminder of the instructions was also displayed on the screen before starting the experiment.

The trial sequence is illustrated in Fig. 5.2. At the beginning of each trial, a red cross appeared at the center of the computer screen to signal the participant to press the spacebar: this caused the presentation of the distractor disk on the center of the screen. The participant was required to maintain fixation on the screen center without taking any action (distractor phase). The distractor lasted for 3 s and was followed by a go-signal informing the participant to go on with the trial. The participant pressed the spacebar again, but this time held it down as long as needed to observe the target disk and prepare the appropriate grip. At this spacebar press, the target disk was displayed on the center of the computer screen (target onset), recording of the PRT for the current trial was initiated, and MATLAB issued a trigger to the EEG marking the onset. Then, once ready to perform the appropriate grip (i.e., the pincer grip for small disks and the pentapod grip for large disks), the participant released the spacebar and pantomimed a grasp towards the on-screen disk. Pantomime grasps were defined as hand gestures whereby the hand approached the screen until the fingers contacted the contour of the disk, as they would do in an actual grasp. At the release of the spacebar, the target disappeared (i.e., the target disk offset, such that participants pantomimed the grasp relying on what they had seen during the motor preparation phase, without online visual feedback about the target), the PRT of the current trial was stored, and MATLAB issued a trigger to mark the target offset. Last, the participant brought back the hand to the starting position and waited for the appearance of the red cross indicating that the next trial could be started (the interval between the target disk offset and the red cross lasted 3 s, giving ample time to the participant to perform the movement). The experiment lasted about 1 h, plus approximately 30 min for setup including fitting the EEG cap.

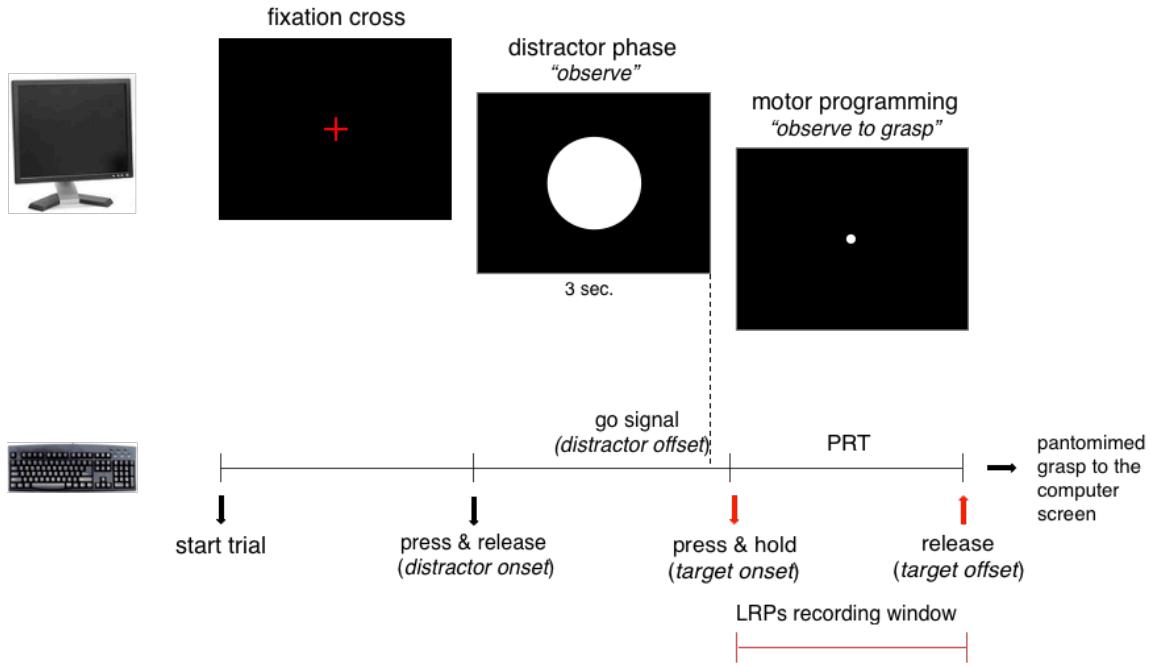


Fig. 5.2. Structure of trials. The fixation cross and stimuli were presented on a monitor. The space key on a computer keyboard was used to record keypresses and releases.

EEG data acquisition and pre-processing

EEG data was recorded from 64 electrodes using an Active Two amplifier system (BioSemi, Amsterdam, Netherlands, <http://www.biosemi.com>). Electrodes were positioned according to the extended 10-20 system (Nuwer et al., 1998). To record the vertical (VEOG) and horizontal electrooculograms (HEOG), four additional leads were placed above and below the left eye and on the outer canthi of the left and right eyes. EEG from all channels was acquired concerning the common mode sense (CMS) electrode at a sampling rate of 512 Hz. Pre-processing procedures were run in MATLAB by means of the EEGLAB toolbox (Delorme & Makeig, 2004; version 14.1.2b) and custom scripts. First, the continuous EEG was split into epochs offline. Stimulus locked epochs began 100 ms prior to target onset and ended 1000 ms following target onset. Stimulus-locked ERPs were aligned to a 100 ms pre-onset onset baseline. Response-locked epochs began 1000 ms before the initiation of the response, and ended 200 ms after the movement onset, and

were aligned to a 100 ms baseline from 1000 to 900 ms prior the movement onset. ERPs waveforms of each trial for each participant were digitally filtered (second-order zero-phase-lab band filter, 0.1–25 Hz), and the filtered individual ERPs waveforms were obtained averaging relevant trials for each condition. Then, EEG artifacts were removed using the SCADS procedure with standard parameters (Junghghöfer et al., 2000; Gruss and Keil, 2019; Harrison et al., 2015; Johnen & Harrison, 2019). This procedure detects individual channel artifacts and then transforms the data to average reference to detect global artifacts. Epochs that contained more than 10 unreliable electrodes were excluded from analysis based on of the distribution of their amplitude, standard deviation, and gradient. For the remaining epochs, data from artifact-contaminated electrodes was replaced by a statistically weighted spherical interpolation using the complete set of channels. Across all participants and all conditions, the procedure rejected approximately 30% of epochs as contaminated.

ERPs analysis

LRP's for right hand movements were measured by calculating the difference between potentials at the C3 and C4 channels (C3-C4; Smulders, Miller, & Luck, 2012). The target-locked P300 was scored at the Pz electrode. For the LRP and P300 components, we derived both amplitude and latency measures. To this aim we adopted different strategies depending on the type of ERP component. The LRP amplitude is known to reflect variations in the amount of inhibition involved in the response, with greater amplitudes reflecting a greater lack of inhibitory success (for instance, see DeJong et al., 1990). The LRP waveform usually consists of an early, quasi-zero trace followed by a later, monotonous negativity reaching the peak negative amplitude. There is some evidence that the temporal location of onsets and peaks in LRPs can vary depending on task manipulations (for instance, see Falkenstein et al., 1994). Thus, we computed amplitudes, onsets, and peaks

by different methods to examine whether results were robust to changes in estimation approaches.

Estimation based on averaging from the raw data

In a first approach, we estimated amplitudes, onsets, and peaks directly from each participant's raw data. The LRP amplitude was then defined as the average μ V value of the area under the curve within appropriate time windows both for pincer and pentapod grips, chosen by visual inspection of individual potentials. Temporal locations of LRP onsets and peaks were also detected within appropriate time windows based on visual inspection (see Results section for details). The LRP onset was defined as the millisecond at which the waveform reached the maximum (MAX) amplitude value; the peak, instead, was defined as the millisecond at which the waveform reached the minimum (MIN) amplitude value. The advantage of estimation based on the raw data is that no assumptions, modelling, or transformations are involved. Random fluctuations between participants can however affect the ability to reliably estimate the temporal locations of specific features such as onsets and peaks.

Estimation based on averaging, segmented regression, and jackknifing

In a second approach to the LRPs analysis, we applied a segmented regression procedure (Schwarzenau et al., 1998). In standard approaches, LRPs onsets are estimated detecting the time at which the amplitude exceeds an absolute or relative criterion (i.e., for instance, at -1μ V or at the 80% of the maximum amplitude, Ulrich & Miller, 2001). However, these strategies are arbitrary and do not work well in the presence of task-related differences in LRP waveforms. In contrast, fitting a segmented regression is less arbitrary in that the whole LRP waveform is used to estimate timings (Schwarzenau et al., 1998; Mordkoff & Gianaros, 2000). We defined the onset as the knot of the fitted segmented regression whereby the potential started to decrease and continued to decrease, and the peak as the knot where the potential reached

the minimum amplitude value before turning back towards zero. The number of knots was chosen from visual inspections of grand average waveforms. Segmented regressions were fitted using the “segmented” package in R (Muggeo, 2008). To model individual differences, segmented regression was combined with a jackknife procedure (Miller et al., 1998; Ulrich & Miller, 2001; Miller et al., 2009). In the jackknife, n subsamples of LRP grand averages are computed by successively omitting from each subsample the LRP data of a different participant, n being the number of participants (in our case, 22). The LRP onset and peak latency were therefore estimated by fitting a segmented regression to each participant's jackknifed grand average. The whole procedure was applied both to the R-LRP and S-LRP data.

P300 analysis

For the P300 component we measured amplitude and peak latency. Grand average waveforms were computed by averaging individual potentials, then a spline smoother was applied. Amplitudes were defined as the average μV value of the area under the curve within an appropriate time window chosen by visual inspection of grand average waveforms. In contrast to LRPs, for P300 components we estimated peaks as the unique ms values at which the waveform reached its maximum (see Results section for details).

Statistical comparisons

Because ERP datasets are rich in random fluctuations, there is a relatively high risk of observing false positives (Luck & Gaspelin, 2017). This is especially true when making comparisons within many factors or performing several pairwise comparisons (Brandstätter, 1999; Steiger, 2004). Accordingly, we sought to avoid unnecessary comparisons and limited the analysis to our specific predictions (see also Brenner, 2016). To this aim, whenever appropriate we fitted multilevel linear mixed-effect models (LMM) using the *nlme* package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). In comparison to traditional linear modelling, which uses ordinary least-

squares, mixed-effects modelling uses maximum-likelihood estimation. This allowed us to predict participant-by-participant variation in model parameters (called random effects) and to discount these individual differences to compute within-participant confidence intervals around estimates of fixed effects, while avoiding drawbacks typically associated with traditional models, such as deficiencies in statistical power, individual differences in repeated measures designs, and unprincipled ways of dealing with heteroskedasticity and non-spherical error variance (see Baayen et al., 2008). In addition, but not less important, mixed-effects modelling allowed us to dispose of null-hypothesis testing, in accord with current recommendations on analytical approaches in psychology and behavioural neuroscience (see Cumming, 2014; Kline, 2004). Thus, for all dependent measures (PRT, LRP, and P300), we compared incongruent conditions with their corresponding (congruent) baselines by constructing appropriate confidence intervals (CIs) around estimates of central tendency. For estimates derived from jackknifing, which compare variation in the quantity of interest across subsets of the total sample instead of across individuals, CIs around the within-participant incongruent vs congruent means were instead computed using the jackknife standard error formula recommended by Miller et al. (1998). R scripts for modelling all data are available in the Open Analysis document (<https://osf.io/yvsg5/>).

Results

Plots of the individual ERP waveforms and tables resuming the main results are viewable in the Open Supplemental Material document (<https://osf.io/yvsg5/>).

Preview reaction times

Data validation

PRTs were defined as the duration of the discretionary temporal window between the onset and offset of the target disk (i.e., the press and release of the spacebar, respectively). Firstly, we checked the PRT distribution for the presence of anomalous values. A cut-off of ≤ 150 ms was deemed appropriate to identify anticipatory responses. Based on this criterion, a total of 57 PRTs were removed. Then, abnormally long PRTs were identified as those exceeding the following criterion for robust outlier detection (Leys et al., 2013): where abs refers to absolute value, PRT is a vector of preview reaction times, MED is the median of this vector, and MAD is its median absolute deviation. A total of 199 trials exceeded this criterion. Together with trials identified as anticipatory responses, a total of 256 datapoints were discarded (4.85% of the whole PRTs dataset). Thus, all statistics used in further analyses were computed on the validated dataset.

Normalization of the PRT distribution

Fig. 5.3 (upper panel, left) shows the PRT distribution. As is typical for response times, this distribution was markedly asymmetrical (skewness = 1.88) and unbalanced in relation to the relative frequency of cases in the center and in the tails (kurtosis = 6.91). We applied a Box-Cox procedure (Box and Cox, 1964; Osborne, 2010) to identify the best transformation for normalizing the raw data (Fig. 3, upper panel, right plot). This indicated that a logarithmic transformation made the PRT distribution reasonably similar to a normal distribution (skewness = 0.13; kurtosis = 2.94), as shown in Fig. 5.3 (lower panel, left and right plots). Accordingly, the analysis was performed on the log-transformed data. For ease of interpretation, however, estimated effects will be reported after an inverse anti-logarithmic transformation as geometric means expressed in milliseconds. Thus, each participant had four geometric means (i.e., one for each of the four distractor-target pairs). CIs around estimates that are symmetrical above and below arithmetic mean on the log-scale become asymmetrical after the inverse transformation, but retain their usual interpretation.

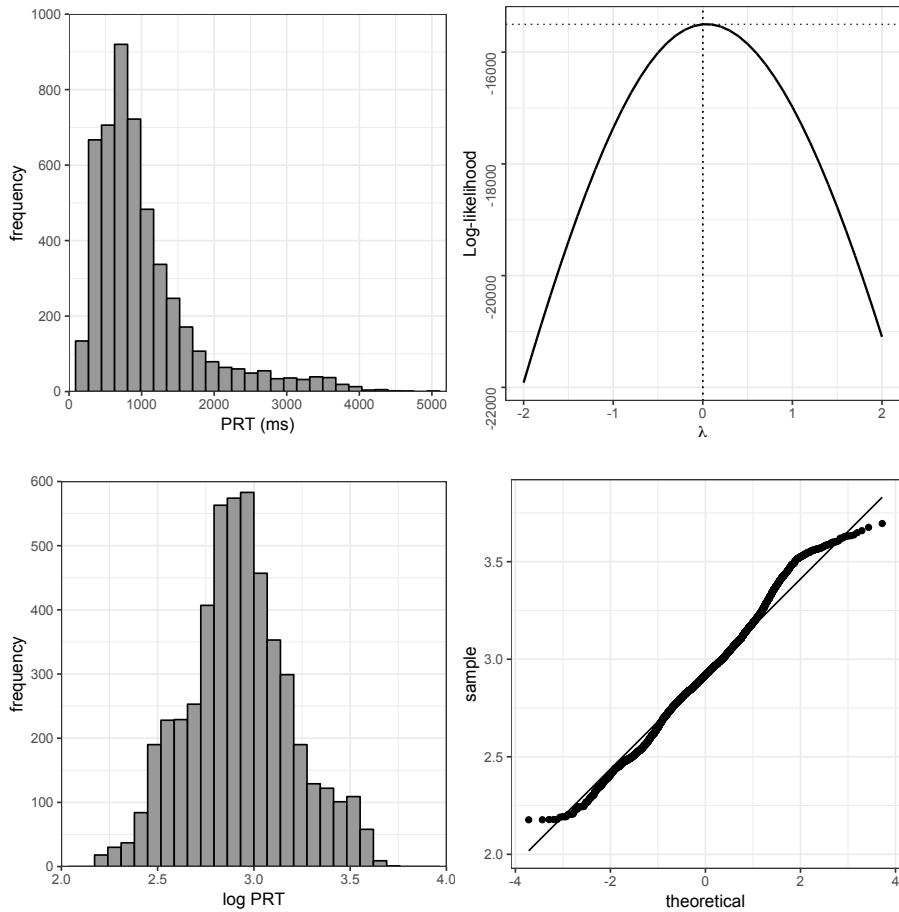


Fig. 5.3. Distribution of preview reaction times before and after the logarithmic transformation. Upper row left: Raw times; Upper row right: Box-Cox likelihood plot suggesting that the best transformation is the log. Lower row left: Log-transformed times; Lower row right: Plot of sample quantiles against theoretical quantiles in a normal distribution.

Within-participant structure of the data

Fig. 5.4 presents individual averages of the log-PRTs in the paired incongruent and congruent conditions, separately for the pincer and pentapod grips. The diagonal line is the locus of no within-participant difference. These plots show that the majority of participants had higher mean PRTs in both incongruent conditions, but this trend was much stronger when the test required a pincer grip. In the congruent conditions, the geometric mean of

PRTs were 788 and 841 ms when participants prepared pincer and pentapod grips, respectively. In the incongruent conditions, they were 848 and 864 ms for pincer and pentapod grips, respectively. Thus, overall PRT were higher in the incongruent conditions than the congruent, and when responding with pentapod than pincer grips.

PRTs modelling

Standard errors for CIs were based the LMM, with condition (i.e., each distractor - target pair) as the fixed-effects factor and participants as random-effects. For model comparisons we performed likelihood ratio tests using Chi-Square (χ^2), following Winter (2013). Model selection was performed as follows. First, we compared the fit of a generalized least squared (GLS) null model with fixed intercept (model 1) with a null model with random intercept (model 2) using a maximum likelihood criterion. Model 2 outclassed model 1, (AIC (1) = 0.21, AIC (2) = -210.2; likelihood ratio (1 vs 2): $\chi^2(3) = 212.83$, $p < 0.0001$), confirming non-negligible interindividual variability in PRTs. Next, we generated model 3 by adding the experimental condition (as a fixed effect) to model 2. The comparison between model 2 and model 3 revealed that the latter provided an even better fit (AIC (6) = -220.68; likelihood ratio (2 vs 3): $\chi^2(6) = 16.06$, $p = 0.001$). That is, comparing model 3 to model 2 supported the conclusion that PRT's varied not only between participants but were also modulated by the type of distractor - target pair (congruent or incongruent). The insets of Fig. 5.4 present LMM estimates of such fixed effects and their 95% CIs. Comparisons can be performed by evaluating whether CIs of the effects cover their corresponding baseline.

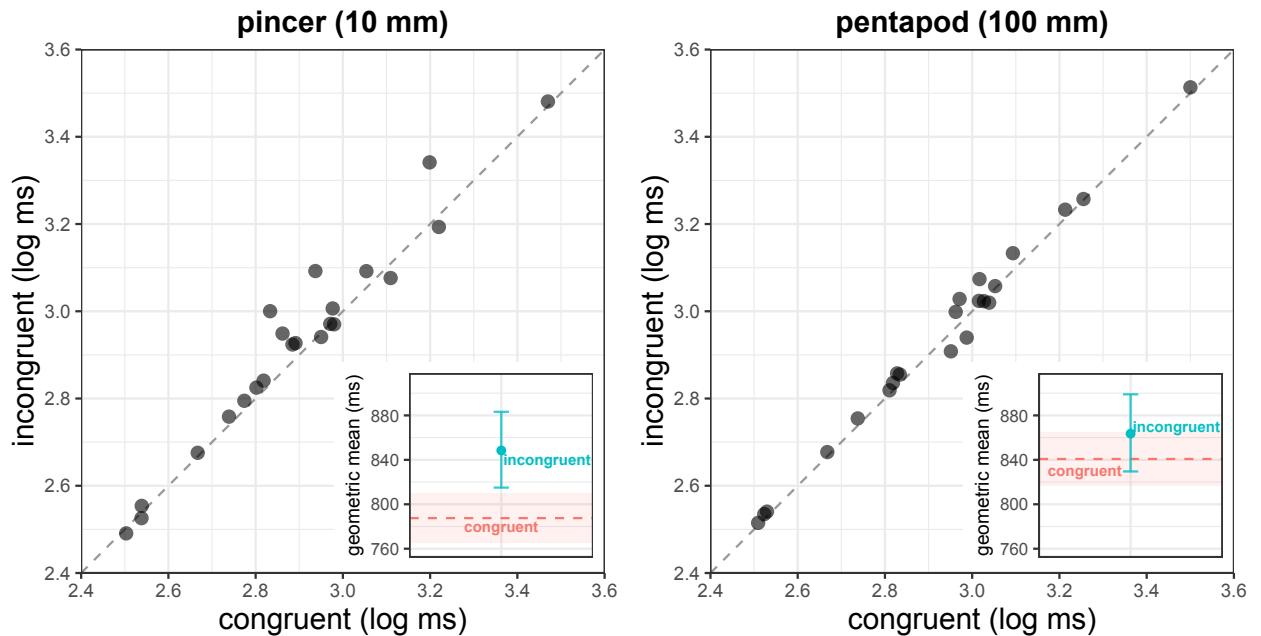


Fig. 5.4. Main plots: Within-participant structure of the PRT data. Each datapoint represents the arithmetic average of pincer or pentapod log-PRTs of one participant, in the paired congruent and incongruent conditions. The diagonal line represents the no within-participant difference (average congruent = average incongruent). Insets: LMM-based 95% CIs around estimates of central tendency (geometric means) in the incongruent conditions (blue disks with error bars), plotted against the equivalent estimates for the baseline (congruent, red) conditions.

Response-locked lateralized readiness potentials (R-LRPs)

Given that we predicted an effect on response-related LRP, we start by presenting the findings of the R-LRPs analysis. Next, we present results of the S-LRP. We conclude with the analysis of the P300 component.

Grand average waveforms

Fig. 5.5 presents R-LRP grand average waveforms (thick curves) obtained by averaging the individual potentials and applying a smoother. Grand averages exhibited a slow negative trend over time, confirming that motor preparation occurred prior to response onset. For pincer grips (left plot), the two

waveforms had approximately the same amplitude and time course from -1000 to -200 ms; then, the R-LRP of the test condition peaked later and the amplitude reduced, compared to the baseline condition. For pentapod grips (right plot), instead, the R-LRP of the congruent condition became negative around -600 ms, whereas the R-LRP of the incongruent condition became negative later around -400 ms; in contrast, both conditions appeared to peak around -150 ms. Finally, the amplitude of the test condition reduced in comparison to the baseline condition.

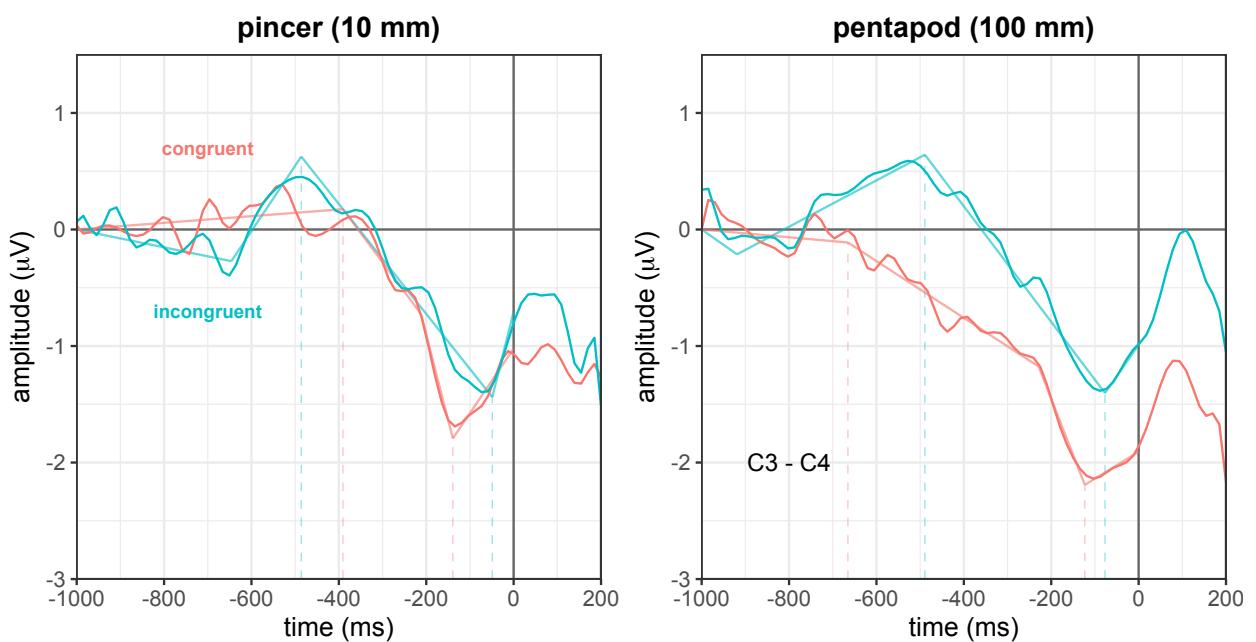


Fig. 5.5. R-LRP grand average waveforms (thick curves) and average jackknifed segmented regressions (thin lines) as a function of grip (pincer, left panel; Pentapod, right panel) and congruence (congruent, red; incongruent, blue). Dashed vertical lines: Average value of the onset and peak amplitude latency estimates of subsamples. Vertical black line: Response onset.

Estimation of amplitudes

For each participant's RLRP dataset, amplitudes were calculated as the mean value of the area under the curve within a -400 to 0 ms time window, both for pincer and pentapod grips. We compared incongruent conditions to the

relevant congruent condition for each grip. Thus, each participant had a paired incongruent-congruent amplitude estimate for both pincer and pentapod grip (22 estimates for each distribution).

Amplitude modelling

Statistical differences were evaluated comparing CIs based on the LMM, with conditions as the fixed-effects factor and participants as random-effects. We compared model 1 with model 2 (i.e., fixed intercept vs random intercept), then model 2 with model 3 (i.e., adding the experimental condition as fixed effect). Model 2 outclassed model 1, (AIC (1) = 421.91, AIC (2) = 392.44; likelihood ratio (1 vs 2): $\chi^2(2) = 31.37$, $p < 0.0001$), confirming non-negligible interindividual variability in amplitude. However, the comparison between model 2 and model 3 revealed that this latter did not provide a better fit (AIC (3) = 395.02; likelihood ratio (2 vs 3): $\chi^2(3) = 3.4$, $p = 0.33$). Thus, although amplitudes were affected by individual differences, the distractor-target pair did not introduce modulations. For pincer grips, means and CIs were: $-0.83 \pm -0.65 \mu\text{V}$ for the baseline (congruent) condition, and $-0.64 \pm -0.91 \mu\text{V}$ for the test (incongruent) condition; for pentapod grips, means and 95% CIs were: $-1.47 \pm -0.65 \mu\text{V}$ for the congruent condition, and $-0.83 \pm 0.91 \mu\text{V}$ for the incongruent condition.

Estimation of latencies of onsets and peaks

We sought to determine whether onsets and peak amplitude latencies of incongruent conditions were different from their relevant baseline. For each participant's R-LRP waveform, onsets were extracted within a -600 to -200 ms time window for pincer grips, and within a -800 to -450 ms time window for pentapod grips. Peak latencies, instead, were extracted within a -150 to -50 ms time window for both grips. Thus, each participant had four paired incongruent-congruent latency estimates, yielding four distributions each of 22 estimates (i.e., pincer onset, pincer peak latency, pentapod onset, and pentapod peak latency).

Within-participant structure of onsets and peaks

The within-participant structure of onset and peak latencies is presented in Fig. 5.6, main plots. These plots display two main features. First, the between-participant variability in the timing of onsets (left column) is much larger than the variability in the timing of peaks (right column). Second, and most important for our current purpose, individual datapoints are about equally located above and below the no-difference locus (diagonal line) of pincer onsets (upper left panel), whereas they cluster above it in pentapod onsets (lower left). Conversely, individual datapoints cluster above the diagonal for pincer peaks (upper right), but not for pentapod peaks (lower right). Thus, the graphical inspection of within-participant differences suggested that R-LRPs onset was delayed in the test condition, relative to the baseline, for pentapod but not for pincer grips. In contrast, the peak of the waveform seemed to occur later for pincer grips than for pentapod.

Latencies modelling

As in the previous analysis, we used LMM to calculate CIs. The same model was applied to onset and peak estimates. For onsets, the null model 1 (fixed intercept) was compared with the null model 2 (random intercept). Model 2 did not provide a better fit than model 1, ($AIC(1) = 1120.68$, $AIC(2) = 1122.683$, likelihood ratio (1 vs 2): $\chi^2(3) = 0.00$, $p = 0.99$). Then, model 3 was generated by adding the experimental condition (as a fixed effect) to model 2. Model 3 clearly yielded a better fit compared to model 2 ($AIC(3) = 1080.091$; likelihood ratio (2 vs 3): $\chi^2(6) = 48.58$, $p < 0.001$). For peak latencies, the comparison between model 1 and 2 provided weak support for a difference ($AIC(1) = 867.14$, $AIC(2) = 865.54$, likelihood ratio (1 vs 2): $\chi^2(3) = 3.57$ $p = 0.058$). The comparison between model 2 and model 3 again revealed the superiority of model 3, ($AIC(3) = 862.95$, likelihood ratio (2 vs 3): $\chi^2(6) = 8.6$, $p < 0.05$). Thus, both onsets and peaks were not modulated by interindividual variability but were modulated by the experimental condition.

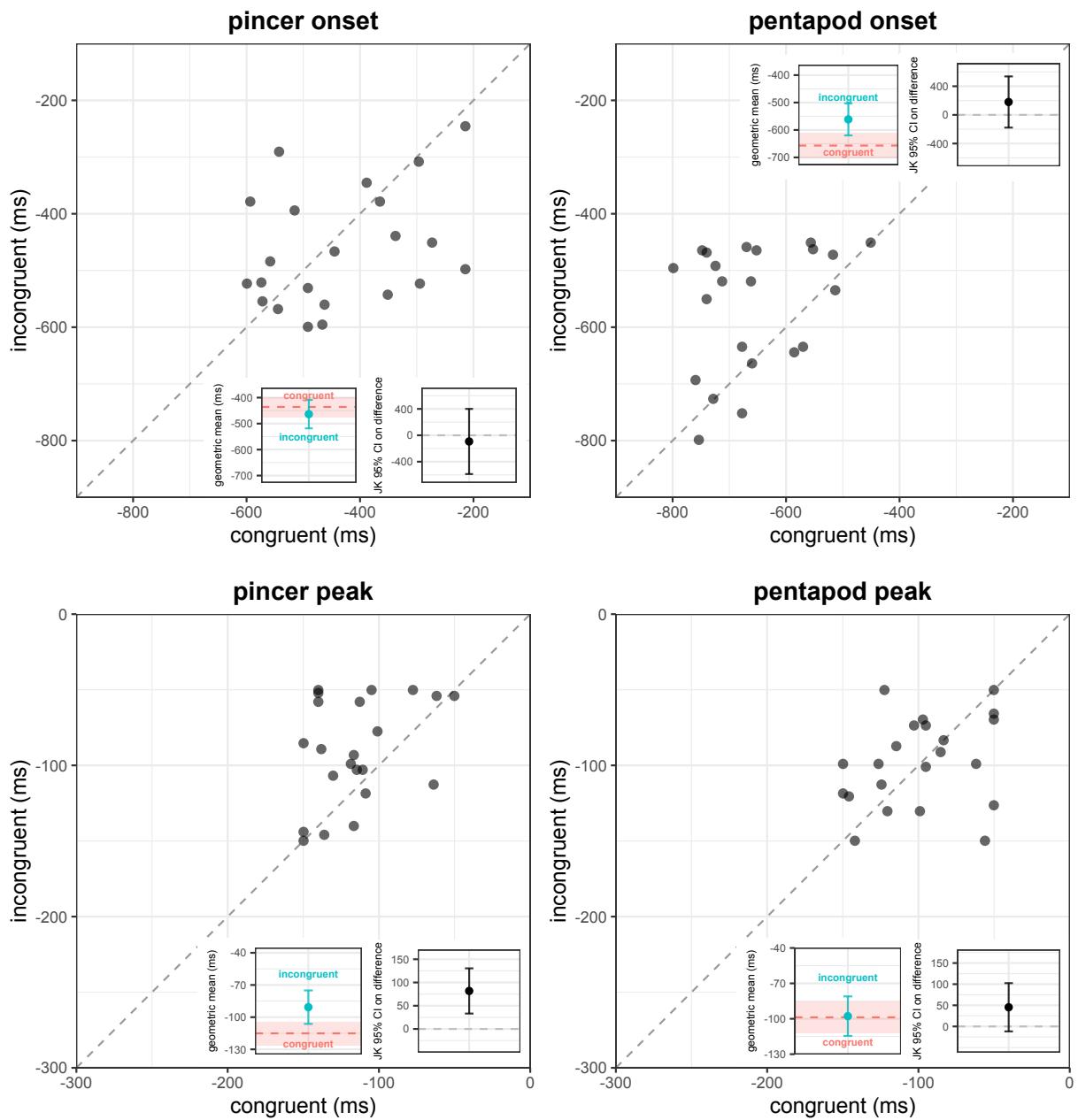


Fig. 5.6. Main plots: Within-participant structure of the R-LRP data. Each datapoint represents the estimated pincer or pentapod latencies for the onset or the peak of the waveform, in one participant, in the paired congruent and incongruent conditions. The diagonal line represents the no within-participant difference (average congruent = average incongruent). Left insets: LMM-based 95% CIs around estimates of central tendency (geometric means) in the incongruent conditions (blue disks with error bars), plotted against the equivalent estimates for the baseline (congruent, red) conditions. Right insets: Jackknife-based CIs on the mean congruent vs incongruent difference.

Segmented regressions on jackknifed subsamples

We performed a second analysis applying the segmented regression method combined with a jackknife procedure (see Methods section for details). First, we computed the 22 R-LRP jackknifed subsamples. Then, we fitted the regressions segmented into three knot-points to best capture the fit of jackknifed subsamples. Superimposed on waveforms, Fig. 5.5 presents average segmented regression fitted on jackknifed participants (shaded lines) as a function of grip and congruence. The average fit was obtained by averaging the individual parameters of each participant's jackknifed fit for each condition. The knots marked by vertical dashed lines represent the average R-LRP onset and peak latency. At least from a visual inspection, the segmented regressions show the same asymmetric pattern seen in the previous analysis.

Estimation of amplitudes

Given that jackknifed subsamples produce estimates that are less affected by random fluctuations, we extended the time window for calculating the average amplitude (from -600 to 0 ms for both grips). As in the raw data analysis, test conditions were compared with the relevant baseline condition for each grip. Thus, each participant had a paired incongruent-congruent mean amplitude value for both pincer and pentapod grips (22 estimates for each distribution).

Amplitudes modelling

Statistical differences were evaluated computing CIs around the mean values of each within-participants distribution. In each comparison, we computed the difference of test minus baseline estimates, then we calculated the standard error of these distributions. Note that in this case standard errors were computed with the formula for jackknifed subsamples (Miller et al., 1998). Resulting means and CIs (95%) were: $0.18 \pm 0.64 \mu\text{V}$ for the incongruent-minus-congruent pincer distribution; $0.86 \pm 0.60 \mu\text{V}$ for the incongruent-minus-congruent pentapod distribution. In contrast with the amplitude analysis

on the raw data, these results revealed that the amplitude in the incongruent condition reduced relative to baseline for pentapod targets after pincer distractors, but not for pincer targets after pentapod distractors or between the two baselines.

Estimation of latencies of onsets and peaks

In each jackknifed subsample the onset and the peak latency were identified as the millisecond corresponding to the knot estimated by the segmented regression. Thus, each jackknifed participant had the same four paired incongruent-congruent latency estimates, yielding four distributions of 22 estimates.

Latencies modelling

In each comparison we calculated incongruent minus congruent differences and then computed the relative standard errors for jackknifed subsamples. CIs were computed around the averages of these incongruent-minus-congruent within-participant distributions. Fig. 5.6 right insets present these CIs for the R-LRP jackknifed latency differences. Comparisons can be directly made by evaluating whether the CIs cover zero. R-LRPs of pincer grips in the incongruent condition peaked later compared to baseline, confirming what we found in the raw data analysis. In contrast, for pentapod grips both onset and peak latency estimates in the incongruent condition were different from baseline. While the two analysis we conducted revealed a consistent pattern for pincer grips, for pentapod grips they do not fully agree suggesting more uncertainty on whether incongruent distractors affected the onset of the waveform.

Stimulus-locked lateralized readiness potentials (S-LRPs)

The two analyses presented above revealed that incongruent distractors delayed the time course of R-LRP waveforms. Thus, this finding supports the idea that the motor system required a cost of updating the first, implicit grip to the second, explicit grip. Nevertheless, we could not exclude that a similar effect influenced the motor program also during an earlier stage of the sensorimotor evaluation of the target disk. Thus, we inspected the LRP potentials as a function of the target disk onset.

Grand average waveform

Fig. 5.7 presents S-LRP grand average waveforms (thick curves) as a function of grip and congruence, obtained by averaging the individual potentials and applying a smoother for a better visualisation. Based on visual inspection of grand averages, there are no differences between the two conditions either for pincer or pentapod grips. Indeed, the onset, which is identifiable at about 100-200 ms, appeared to be almost identical between conditions for both grips. The same is true for the peak latency which is identifiable at about 400 ms. Besides, amplitudes show a large degree of overlap. The absence of any difference is also clear from the average segmented regressions showed in Fig. 5.7 (thin lines). Thus, we ruled it unnecessary to run statistical comparisons.

P300 component

As a last step, we analyzed the P300 component to verify whether earlier attentional processes delayed the motor preparation.

Grand average waveform

Fig. 5.8 presents grand averaged P300 components as a function of grip and congruence. At least qualitatively, the figure suggests that the amplitude in the

incongruent conditions was higher compared to congruent conditions whereas waveforms clearly peaked at the same time. Thus, we ruled it unnecessary to run statistical test on peak latencies and compared amplitudes only.

Estimation of amplitudes

Amplitudes were calculated as the mean value of the area under the curve within a 250 ms to 500 ms time window for each condition and each participant. Thus, each participant had two paired incongruent-congruent amplitude estimates for each grip (22 datapoints in each distribution).

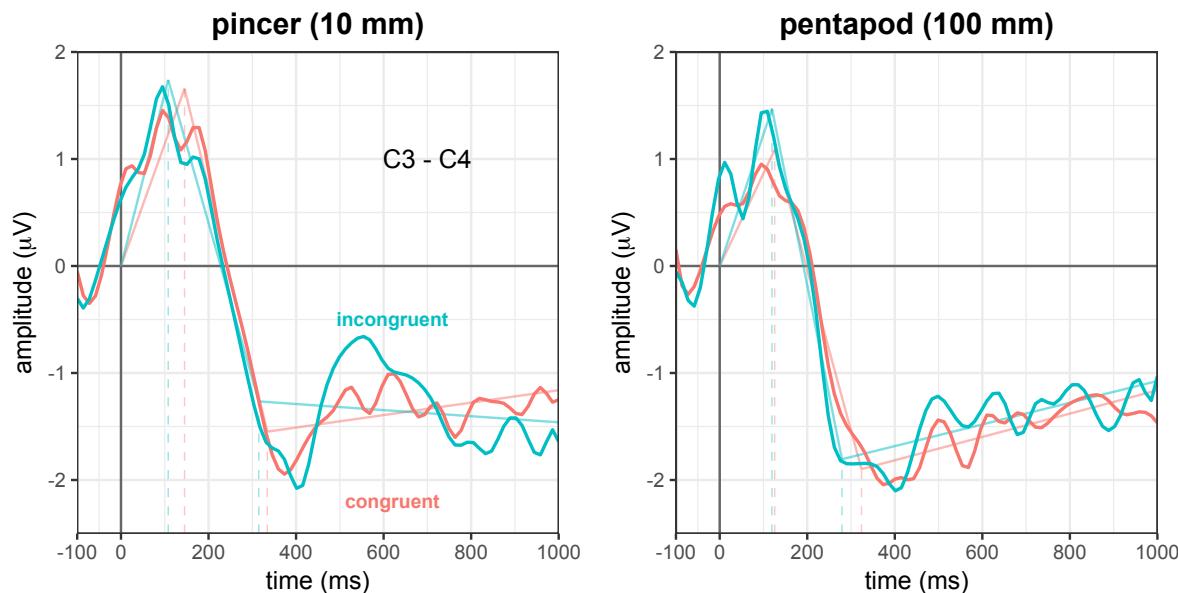


Fig. 5.7. S-LRP grand average waveforms (thick curves) and average segmented jackknifed regressions (thin lines) as a function of grip (pincer, left panel; pentapod, right panel) and congruence (congruent, red; incongruent, blue). Dashed vertical lines: average value of the onset and peak amplitude latency estimates of subsamples. Vertical black line: stimulus onset.

Amplitude modelling

Statistical differences were evaluated with CIs calculated from a LMM. Model 2 (random intercept) outclassed model 1 (fixed intercept) revealing a better fit

(AIC (1) = 381.48, AIC (2) = 341.40, likelihood ratio (1 vs 2): $\chi^2(3) = 42.07$ p < 0.001). Model 3 (by adding the experimental condition) outclassed model 2 and revealing an even better fit (AIC (3) = 325.89, likelihood ratio (2 vs 3): $\chi^2(6) = 21.49$, p = 0.0004). Thus, both interindividual variability and the experimental condition introduced non-negligible modulations in amplitude. Fig. 5.9 presents the CIs around the means calculated in the model: comparisons can be performed directly by evaluating whether CIs of incongruent conditions cover the relevant baseline. The S-LRP and P300 analyses indicated that no reliable delays occurred due to earlier attentional or sensory processes related to the target disk. These results strengthen our interpretation that PRT costs are due to an update of motor preparation.

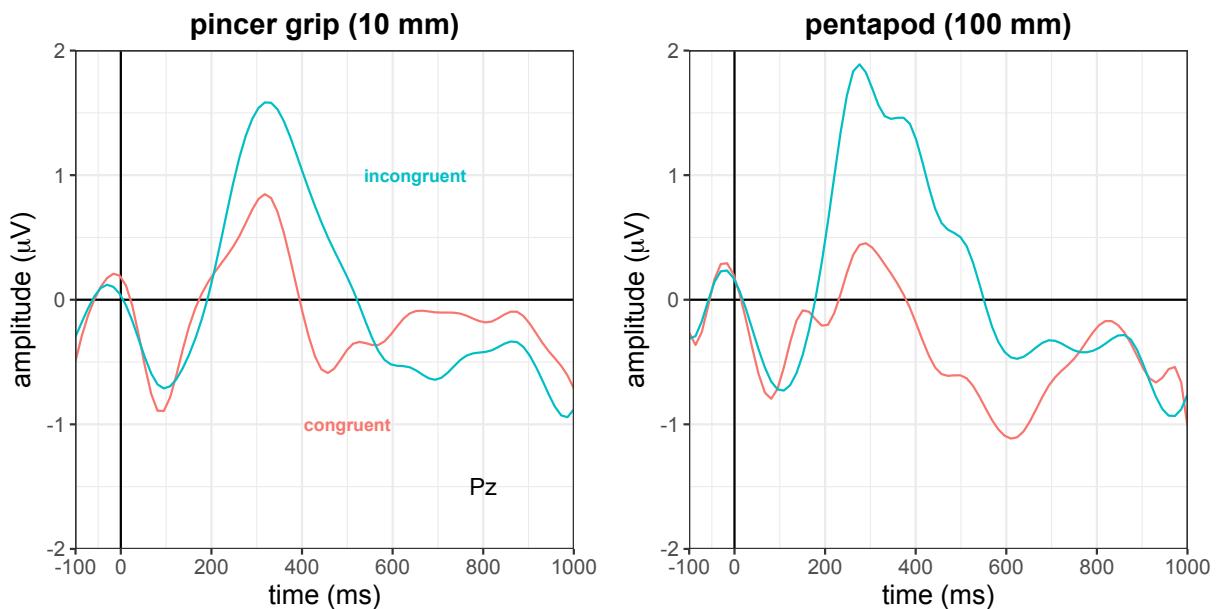


Fig. 5.8. P300 component grand averages as a function of grip (left, pincer; right, pentapod) and congruence (red, congruent; blue, incongruent). Vertical black line: stimulus disk onset.

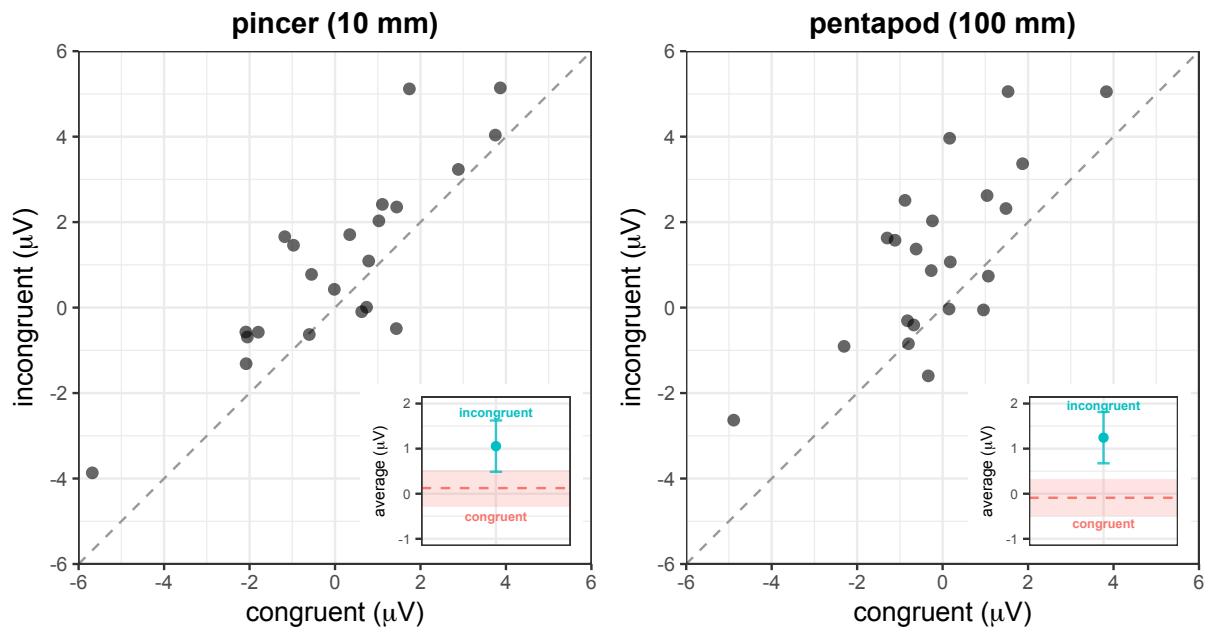


Fig. 5.9. Main plots: Within-participant structure of the P300 data. Each datapoint represents the estimate of pincer or pentapod amplitude of one participant, in the paired congruent and incongruent conditions. The diagonal line represents the no within-participant difference (average congruent = average incongruent). Insets: LMM-based 95% CIs around estimates of central tendency (average) in the incongruent conditions (blue disks with error bars), plotted against the equivalent estimates for the baseline (congruent, red) conditions.

Discussion and conclusion

According to the TVSH, vision-for-action continuously updates visual information to support the control of actions in real time. This implies that visuomotor codes elicited before an action (i.e., the temporal context) should be rapidly overwritten by codes relevant to the current motor response. For instance, representations elicited by viewing a distractor object would not modify motor preparation parameters (i.e., in our case, the PRT) for grasping a successive target object. To test this prediction, we analyzed PRTs, LRPs, and the P300 component during a pantomimed grasping movement directed to a target disk preceded by a different distractor disk. Our results provide, for the first time, consistent behavioural and electrophysiological evidence that previous implicit visuomotor processes interact with motor preparation for a

successive actual action on a different object. Key implications of our findings are discussed below.

The effect of distractors on PRTs is asymmetric

The time participants spent observing the target and preparing the response depended on the size of the previous distractor disk. When distractors and targets were different in size, PRTs were longer overall, but there was a notable difference between trials calling for pincer vs pentapod grips. After a large distractor, PRTs associated to pincer grips involved a large cost (i.e., the PRT was considerably longer). After a small distractor, in contrast, PRTs associated to pentapod grips involved only a relatively small cost with weak statistical support for a difference with the baseline. These results are very similar to those of Pisu et al. (2020) and support the notion that seeing the distractor affected the preparation of the response for the test. This distractor effect, however, appears to be qualitatively different from classical visuomotor priming in that the observed cost for incongruent distractor-test pairs (which is predicted by visuomotor priming) is much larger for small disks after large distractors than for large disks after small distractors. The effect of distractors on PRT's is therefore asymmetric, unlike standard visuomotor priming which predicts a symmetric effect of congruency. After considering several possible accounts of their results, including visuomotor priming and finger-based facilitation, Pisu et al. (2020) proposed that their results may be due to asymmetric generalization of precision when setting motor parameters in an action's planning phase. The current results are consistent with this possibility.

R-LRPs also revealed an asymmetric effect, but S-LRPs and P300 components did not

We sought to determine if PRT costs corresponded to differences in LRP s, which are ERP signatures of movement preparation. Based on asymmetric generalization of precision, one would expect a delay in some component of the R-LRP waveform when preparing a pincer grip after a large distractor, but

a negligible or at least weaker delay in the opposite condition. Our results indicate that one such delay is measurable for the negative peak in the late part of the waveform. Specifically, when responding with pincer grips, the peak amplitude of the R-LRP waveform occurred later after an incongruent (i.e., large) distractor than it did after a congruent (i.e., small) distractor. When responding with pentapod grips, conversely, the peak amplitude occurred at about the same time with both distractors. In contrast, when using pentapod grips the onset was delayed after the presentation of a smaller distractor disk, whereas the peak latency was relatively unaffected. Moreover, in contrast S-LRPs did not show differences between congruent and incongruent conditions and both grips. This suggests that early perceptual processing evaluation of the target features was not affected by the pre-activated motor program. Furthermore, the analysis of the P300 components revealed higher average amplitudes in incongruent conditions than congruent. This is consistent with the idea that updating visual information recruited additional attentional resources. However, P300 components peaked at the same time in both conditions and both grips. Hence, the contextual updating associated to incongruent distractor - target pairs did not further modulate attentional processes. Taken together, these results confirm that implicit processing related to the distractor presentation did have an effect on the preparation of the pantomimed grasp for the test object and, at least under these conditions, this effect was most likely due to motor rather than sensory or attentional processes.

Caveats and limitations

One important difference between the protocol employed in the current study and that of Pisu et al. (2020) is that in their case participants performed an actual grasp directed to a solid three-dimensional disk and picked it up at the end of the response. Here, instead, participants performed a pantomimed grasp towards a disk that was drawn on a computer screen. Although they moved the hand towards the screen rather naturally, in the final part of the

grasp they could not pick up the disk as in Pisu's study. The impact of these differences on the interpretation of the current result is, at present, not completely clear. Goodale et al. (1994) and Westwood et al. (2000) suggested that pantomimed actions involve interactions of ventral stream processes with dorsal visuomotor processes, while actual object-directed actions depend solely on dorsal circuits. However, an fMRI study showed that pantomimed grasps can recruit dorsal neural circuits, as do real grasps (see Króliczak et al., 2007). Whether this is true for all pantomimes and for all phases of an action is also presently not clear. In our study, we focused on motor preparatory processes, and one feature of our data suggests that the pictorial nature of our 2D stimuli might have affected motor preparation. In the congruent conditions, PRTs were longer for pentapod than for pincer grips (compare the pink bands in Fig. 5.4). This is the opposite of what was observed by Pisu and collaborators, and of what one would expect based on the precision which is presumably required in a motor program aimed at a large vs a small object. The latter should require a more precise program, which in turn might be expected to imply longer preparatory processing. We are currently designing further studies aimed at testing possible differences between preparation and execution of pantomimed or real pincer and pentapod grasps. As suggested by an anonymous reviewer, this could be done by combining the EEG with augmented reality to create a virtual 3D object or, in alternative, with a procedure for displaying actual three-dimensional objects. We stress however that, even if the current effect did involve a contribution from the ventral system, this would weaken its implications for the dorsal amnesia hypothesis (see Introduction), but would not undermine our conclusion that the mere sight of the (irrelevant) distractor modulated R-LRPs during motor preparation. This finding provides useful insights into the nature of potential temporal interactions within cortical networks for motor planning (Castiello, 2005; Schenk et al., 2011; De Sanctis et al., 2013; Budisavljevic et al., 2018).

Chapter 6

General Discussion and Conclusion

The research presented in this thesis sought to expand the current knowledge of how the motor system codes sensory information for representing the size of objects. According to the TVSH, vision-for-action is immune to stimulus-contextual effects in contrast to vision-for-perception, resulting in a dissociation between motor and perceptual responses. In general, this assumption is based on results showing that a motor response such as grasping is programmed on absolute rather than relative information, both in space and in time. This belief that represents a crucial issue in the cognitive neurosciences on motor control. Throughout four experiments, I investigated whether motor and perceptual responses dissociate from the Uznadze illusion. According to the results of these experiments, overall the answer to the question is negative: Motor responses are programmed relying on relative spatiotemporal information rather than absolute. In this last section, I briefly summarized the findings of each experiment and draw a general conclusion.

Summary of the experimental findings

Chapter 2. Previous studies on action-perception dissociations employed visual illusions in which the illusory effect emerged by presenting the test object juxtaposed to an array of inducing stimuli (such as, for instance, the Ebbinghaus illusion). In contrast, in the Uznadze illusion a size-contrast effect emerges by presenting two objects having different sizes in sequence. In this first work, I compared motor (MGA) and perceptual (ME) responses to the Uznadze illusion in a standard experimental setup. The main aim was to test whether MGAs were affected by the temporal context. Results revealed that both MEs MGAs were affected by the size of inducers, i.e. size representation was sensitive to the temporal context. Moreover, illusory effects for both responses decreased when inducers differed from tests, suggesting size representations are affected by similarity. These findings represent the first solid evidence that motor and perceptual responses do not

dissociate in the Uznadze illusion, in turn suggesting that vision-for-action codes size relying on relative rather than absolute information.

Chapter 3. In this second work, the Uznadze illusion was further manipulated to explore novel and intriguing research questions. First, I investigated whether presenting inducers haptically might had an impact on perceiving the size of the test object. Using the same temporal presentation, participants inspected visually or explored haptically large o small inducers before the presentation of tests. Moreover, I also manipulated the spatial congruency of the inducing-induced pair of objects, presenting them in the same (congruent) or a different (incongruent) position relative to the test. Results revealed that perceptual (intermanual match, IMM) and motor responses (MGA) may or may not dissociate depending on which sensory channel and spatial position the inducers were presented in. With visual inducers, IMM and MGA did not dissociate: Both responses showed the Uznadze size contrast in congruent conditions and no size contrast effect in incongruent conditions. With haptic inducers, instead, IMM and MGA did dissociate. MGAs showed either a null effect or the inverse pattern of the Uznadze illusion (i.e., larger or smaller MGAs after large or small inducers, respectively) depending on spatial congruency. This is a compelling finding that is not easily explainable in terms of distinct size representations between perception and action. I discussed that these results are best explained in terms of multisensory integration and modification of the internal hand schema.

Chapter 4. The experiment of this chapter investigated the time course of motor preparations in grasping. Here, the focus was on the preview time when preparing the grasping (PRT). According to the TVSH, motor representations in the dorsal stream are continuously updated second-by-second on here-and-now information. However, this hypothesis is not supported by the results of this experiment. Here, participants grasped test objects of different sizes, each matched with a specific grip, after having seen a larger, smaller, or equal

distractor object. PRTs were longer for preparing the grasp when distractors were larger than the test, but not when they were smaller. This finding suggests that large distractors elicited a first motor representation that caused a cost for updating the upcoming grasping for the test. Conversely, small distractors did not introduce PRT costs. Thus, these results are best explained by an interaction occurring at the level of sensorimotor processes that generalizes the precision involved by the size of objects. Accordingly, a first motor representation does not decay immediately but can rather affect a second, upcoming representation of a successive action.

Chapter 5. This last work sought to corroborate the findings of the previous experiment. Here, I investigated event-related potentials (ERPs) for grasping a test object after the presentation of distractors equal or different in sizes. In particular, the lateralized readiness potential (LRP) is an online cortical index of motor preparation. Results revealed consistent behavioural and psychophysiological data: PRTs were longer for grasping the test after the presentation of large distractors and associated with displacement in time of specific LRP components. Such LRP modulations provide of evidence that visuomotor information presented before a grasp does affect how we will perform that grasp, in contrast to models that assume a short-memory of motor representations in the dorsal stream.

Conclusions

Whether perception and action operate with similar internal representations is a long-standing debate in the cognitive neurosciences. This dissertation aimed to answer the following general question ‘is the motor system sensitive to sensory information presented recently?’. Although this question will requires further research, the experiments presented in this thesis demonstrate that the motor system is actually affected by previous spatiotemporal information. Both finger aperture and time preparation for

grasping a test are not computed only on the available information of the test, but are rather sensitive to the size of previously presented objects. This finding is a novel piece of information about visuomotor processes in grasping that deserves to be further studied.

Finally, the Uznadze illusion draws to be a powerful and reliable tool for testing action-perception dissociations. More in general, inducing stimuli in a sequential presentation might reveal further valuable insights into how visuomotor processes code sensory information for guiding actions.

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Biographical sketch

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